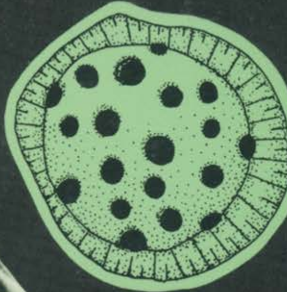
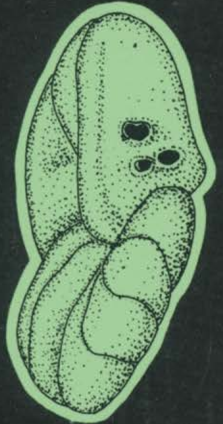
Foraminifera

John R Haynes





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‘Let us not be too entirely mechanical, Baconian, and experimental only.’

Richard Jefferies

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Preface

The last general textbook on Foraminifera published in Britain was that by Chapman in 1902. This may appear surprising in the light of their value in geological work and their emergence 'as perhaps one of the most abundant organisms on earth by virtue of their abundance in the deep sea' (Lipps, 1978). It is explained by the success of Cushman's book on Foraminifera published in the United States in 1928 which went into several editions, the last in 1948, and by their excellent coverage in Glaessner's *Principles of Micropalaeontology* (1945). Both these books are now out of date and out of print. Foraminifera have been covered in the encyclopaedic monographs on invertebrate palaeontology published in several countries since World War II, the treatment by Loeblich and Tappan (1964) in the *Treatise on Invertebrate Paleontology* being the best known, but with an inevitable emphasis on classification. Their Recent distribution has also been well covered (Murray, 1973b). There is, therefore, a real need for a general textbook on Foraminifera which lays stress on their stratigraphical application.

This book is designed as an advanced text for undergraduate students in palaeontology and for postgraduate students reading MSc courses in micropalaeontology or embarking on research into Foraminifera. However, the introductory chapter is written for the beginning student who may be considering taking options in palaeontology later. Chapters 2 to 5 also contain a number of sections which should be of general interest to students of geology and palaeontology.

Foraminifera offer a number of peculiar advantages as a basis for introducing micropalaeontology to undergraduates. Samples are easy to obtain and methods of preparation simple, while examination can be carried out with relatively cheap binocular microscopes. Project work involving collection from outcrop or from Recent sediments in marshes or estuaries can be arranged without too much difficulty. It is thus possible to teach large classes without recourse to multiplication of specimens by making plaster casts or using photographs.

Foraminifera also have the advantage that they span the entire stratigraphical column. Study of the application of the different orders which succeed each other in time involves the student in a tour from the Cambrian to the Recent and brings him up against many of the fundamental problems of earth history. On the other hand, a single order may be studied with profit. For instance, the interest of geography students taking geology as a second subject can be caught by exposing them to the problems of using planktonic Foraminifera in palaeoclimatology.

This book could not have been written without the co-operation of other members of the Geology Department in Aberystwyth, and I am grateful to all those who have helped in its preparation. In particular I must thank Professor Emeritus Alan Wood for his constant encouragement and for reading the entire manuscript. Dr Denis Bates read chapters 1 to 5, Dr Ben Johnson chapters 6, 7 and 9 and Dr Glyn Pearce read chapter 10, while Dr Graham Jenkins and Mr Nick Holmes read chapter 14. I have incorporated many of their suggestions but it should be clear that any mistakes are my own. My heartfelt thanks also go to Mr Howard Williams for his skilful photographic work, to Mr Arnold Thawley for drafting the text figures and to Mr Gordon Rattray for making thin sections. Miss Alicia Moguilevsky took the scanning electron micrographs and, together with Mrs Chris Chadwick, checked the references and abbreviated them according to the *World List*; Mrs Marian Rivers typed the manuscript, and Mrs Pat Jones the references and many of the tables and text figures.

Finally, I must express my gratitude to my long-suffering family for cheerfully accepting the loss of all my 'spare time' and to my wife for her warm support when my spirits flagged.

Aberystwyth, 1981 J.R.H.

Chapter 1

The Scope of Foraminiferal Studies

> A palaeontologist, writing about their dead shells, would have no scruples in entitling them 'Famous Fossils'.
>
> (Sandon, 1957)

A possible title considered for this textbook was 'The Geological Uses of Foraminifera'. Certainly no other group of fossils is more important to the geologist, and the majority of palaeontologists employed in industry and oil exploration are specialists in Foraminifera. As a perusal of the 'Index and Bibliography of Micropalaeontology' will show, over 500 scientific articles are published each year on this group alone. This is a direct reflection of their importance in the economic field. But their fame rests equally on the attraction of their exquisite architecture to the artistic and scientific mind. Indeed, the early microscopists frankly disavowed any utilitarian intent and this attitude was strongly endorsed by Walker and Jacob (1798) in the earliest British study of Foraminifera with scientific (Linnean) nomenclature. This work includes the following quotation:

> Let not the minuteness of the objects here delineated call up the surly enquiries of those who have not been accustomed to live with their eyes open to the works of nature: they are not fit judges in this matter. If they will persist in asking 'Of what use is all this labour? What good can accrue to mankind from this knowledge, in point of food or other use?' We know of none at all, either present or likely to happen, as to the body, for use or ornament, or to the satisfying any appetite: nevertheless, a much nobler idea will take its rise in our opinion; one which, by displaying so momentously the power of the omniscient Creator, will thwart the infidel in his favourite ideas of escaping the eyes of the almighty, and force him as he descends the scale from the more immense objects to these minutissima, to confess, that the being which has formed these, can fully equal all that the tongue of man has yet declared of the possibility of his power. For what a train of wonders have we here to pursue? What must be the economy of animals so very diminutive, so weak, so exposed from their situation to the force of every rude wave, and who notwithstanding, so often escape unhurt? How do they rear their young? From whence collect their prey?

Two hundred years of research were to be devoted to these questions but, ironically, only a few years were to elapse before William Smith, early in the nineteenth century, demonstrated the stratigraphical usefulness of fossils and Foraminifera became prominent in classical palaeontology. But delight in their intricate beauty of form, so remarkable in a single-celled animal, has remained a mainspring of research into Foraminifera to our own day. This is shown by the signal contribution made by amateurs: Brady—a chemist, Flint—a surgeon, Wright—a grocer, and Earland—a post office official. Fortunately, despite the advent of expensive aids to research like the transmission electron microscope (TEM) and the scanning electron microscope (SEM), Foraminifera can still be effectively studied with quite simple equipment and amateurs can still play their part.

The complexity of shell structure in Foraminifera which attracted the early microscopists is also the basis of their geologic use. Simple forms appeared in the Cambrian and dominate the Lower Palaeozoic. The subclass became abundant with the evolutionary development of relatively large and complicated test architecture by the late Palaeozoic, and new families continued to appear through the Mesozoic and Cenozoic (figure 5.3). This long and well-marked evolutionary record makes Foraminifera of outstanding value in zonal stratigraphy.

An incident aptly illustrating this aspect of the geological utility of Foraminifera occurred during the drilling of the Mochras Borehole on the shore of Northern Cardigan Bay (Wales), a joint venture between the Department of Geology, Aberystwyth and the Institute of Geological Sciences (plate 4). This borehole was sited west of the Mochras Fault by Professor A. Wood to investigate the previously unknown submarine stratigraphy of the bay by means of a continuously cored section. By March 1968 the drilling had penetrated over 300 m of red and green marls and sandstones of presumed Tertiary age, and the possible age of the next formation likely to be penetrated was debated with some excitement. Estimates ranged from as old as the nearby Lower Palaeozoic rocks of the Harlech Dome, east of the Mochras Fault, to as young as Upper Mesozoic, perhaps even as young as the Upper Cretaceous Chalk. Finally, the news was telephoned from the rig that the borehole had passed through an unconformity and penetrated a grey shale that resembled the Carboniferous shales in the Cheshire Basin. At this time Professor Wood and a number of members of the Department of Geology were away at sea, on the research vessel 'John Murray', carrying out marine, geological and geophysical researches. I therefore passed the news on to them by Radio Telegraph before visiting the rig to collect samples from the new cores for analysis.

Preparation of the core material was simple. The chips struck off the cores by the blows of a hammer were further broken down to pieces about 1 cm in diameter and boiled in water with washing soda. When the shale had broken down to mud the sample was poured through a fine mesh sieve so that the sand-sized material could be retained while the mud was washed away. The sample was then dried and shaken gently through a nest of sieves to separate it into different size fractions for ease of examination.

I first looked at the coarsest fraction under the lowest power (× 10) of a stereoscopic, binocular microscope and after a little searching noticed a triangular shell flake. My first thought was that this could be a fragment of a bivalve or ammonite, but examination under a higher magnification soon revealed that it was a perfect specimen of the foraminifer, *Citharina* (plate 11, nos. 5, 8). This genus first appeared in the lower part of the Jurassic Period in the Liassic Epoch. Immediately it was clear that the shales penetrated by the cores were not Palaeozoic and were most probably early Mesozoic. This was confirmed by the microfauna in the finer fractions of the sample which included numerous other examples of Foraminifera belonging to the family Nodosariidae (chapter 9) and characteristic of the Lias.

Another message then crackled out from the radio station at Holyhead, North Wales to the Aberystwyth party in the storm-tossed research ship—'Forams indicate Lias'—a message no doubt thought to be in code by the operator but vital information for the geophysical investigation of the layers of rock beneath the sea floor.

The reason why Foraminifera are important in oil exploration and other subsurface work as *index fossils* (indicators of a particular geological age) lies not only in their abundance but equally in their range of size. This is generally between 0.10 mm and 1.00 mm and averages about 0.33 mm, equal to the fine sand grade of sediments, although some are macroscopic and exceed 5.00 mm in diameter, 'Larger Foraminifera', and some are smaller than 0.10 mm, 'Microforaminifera'.

The importance of the size of Foraminifera in subsurface work will become clear if we consider the basic technology of exploration drilling. The Mochras Borehole was drilled by a process of continuous coring with cores up to 6 in (150 mm) in diameter. This is very costly and is normally only indulged in by government or international agencies with the necessary financial backing and when a complete stratigraphical analysis is required of particular key sections. An up-to-date example is the United States programme of coring in the major oceans, JOIDES—Joint Oceanographic Institutions for Deep Earth Sampling, now replaced by IPOD—International Programme of Ocean Drilling, with participation by major European countries including Britain. The financial and scientific effort is on the scale of space exploration and radio astronomy and Foraminifera find their place in a general appraisal of the sediments which includes other, very small microfossils (nannoplankton) and the macrofauna such as Mollusca which is also preserved in large-diameter cores.

By contrast, in the hard-headed, cost-conscious world of the oil men the majority of boreholes are the result of rotary drilling with cores taken only at particularly important intervals. The basic technology is outlined in figure 1.1. The oil derrick (named after a notorious hangman of 'Tyburn Tree') supports a 'drill string' of hollow drill pipes with a drilling bit on the end which is rotated like an auger into the ground. The drill string which consists of round, 30 ft (9 m) pipes joined by collars turns freely on a 'swivel' and moves down on a 'travelling block', the weight of the string itself providing the necessary downward force. Rotation is transmitted by a diesel-powered winch ('draw works') via the 'rotary table' which grips a square 'kelly' at the top of the drill string. The bit which is of hardened or diamond-studded

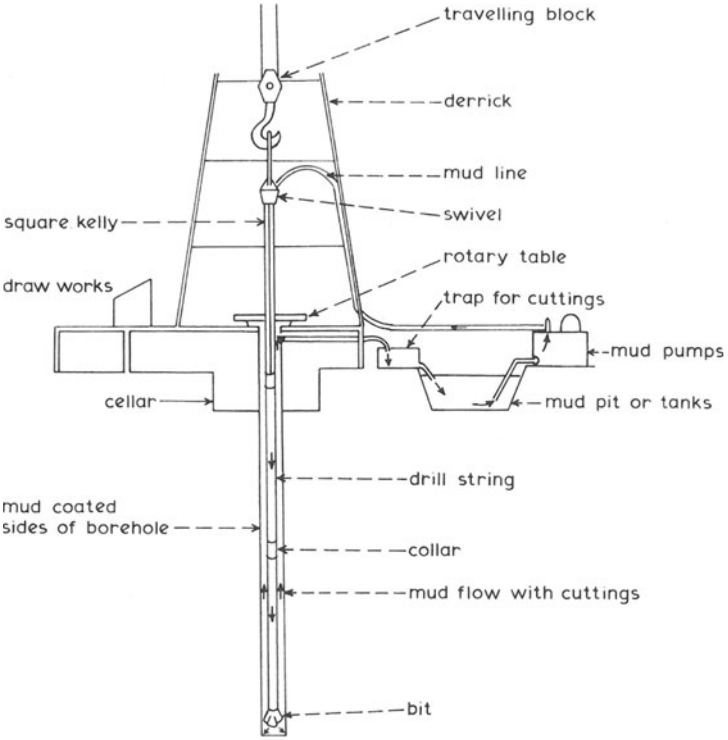

Figure 1.1 The basic technology of rotary drilling

steel is lubricated by a special drilling mud which is pumped down the drill pipe and through the bit to come back between the pipe and the borehole wall. The mud cools and lubricates the bit and provides a seal which helps to prevent the wall of the borehole caving or sloughing off with loss of fluids from the formations that have been penetrated. Not of least importance, the mud carries out the drill cuttings, sometimes called 'ditch cuttings' because in the old days they were simply run off into the ditch to the 'mud pit'. They are now caught in a box or mechanical sieve ('shale shaker') before the mud goes back into the mixing pit. Samples of the cuttings are usually taken to represent every 10 ft (3 m) interval drilled. The necessity for the mud to be of a quality to carry out these functions has called into existence a new tribe of specialists. These are the 'mud sniffers' who study mud chemistry and weight it with minerals such as barytes to counterbalance oil and water pressures. Nowadays this is done in special tanks.

Drilling can be continued until the top of the kelly is at the rotary table. It is then unscrewed and another pipe is winched up and attached before the kelly is replaced and drilling recommenced. Eventually, the drilling bit becomes ineffective through wear and the laborious process known as 'making a trip' supervenes. The whole drill stem has to be winched up and the pipes unscrewed one by one so that a new bit can be added. The pipes are then lowered again, one at a time, back into the hole.

It is an instructive and stirring experience to watch a well-trained and experienced drilling crew in action, whether stripped to the waist under the Saharan sun or padded up against the subzero winter temperatures of the Canadian Plains. The dangerous conditions of the rig floor, slippery with drilling mud, demand teamwork and skilful co-ordination as the 'rough-necks' grapple with the greasy pipes; a false move or inattention can result in a man being knocked down or sent spinning off the platform injured.

As the hole gets deeper, the time it takes to 'make a trip' takes longer. As depths over 10 000 ft (3 km) and even up to 20 000 ft (6 km) are commonly achieved it may eventually take several days and swallow up a considerable proportion (up to one-fifth) of the drilling time. It thus accounts for a considerable proportion of the costs. These can amount to £250 000 for a deep hole on land, and may even reach £1 000 000 on the deeper parts of the continental shelf, as in the North Sea, where expensive drilling platforms or barges costing several million pounds are also required. On average, only one exploration borehole (wildcat) in ten is successful in finding oil, and in the case of the 'dry holes' the samples and various logs of the sections penetrated will be the only result of the expenditure of time, money and effort.

When a core is required it is necessary to fit a special drill pipe with diamond cutting wheels round the rim and a spring device for catching the core. Each time a core is taken it is necessary 'to make a trip'. It will thus be appreciated that both the driller and management will be keen to avoid coring unless absolutely necessary and to drill ahead as quickly as possible by the rotary method. In softer rocks such as shales it may be possible to drill several thousand feet of section before the bit wears out.

For this reason the majority of samples from oil company boreholes are finely crushed ditch cuttings in which only minute fossils such as Foraminifera stand a chance of escaping destruction. The economic application of the study of these fossils in the oil industry has led directly to the rise of 'micropalaeontology'—that is, the study of small fossils which because of their small size when adult require special methods of collection and examination, either by means of the light microscope or by the scanning electron microscope.

It is interesting to note that although the term was apparently coined for the microscopic study of bryozoans in 1875, micropalaeontology, for the oil industry during the early part of this century, became virtually synonymous with the study of Foraminifera and ostracods. This is because Foraminifera, like ostracods, are not only small enough to escape crushing during drilling but large enough to be identified by the same low magnification, wide-field binocular microscopes used by the well-site geologist when looking at ditch cuttings. The expensive methods of extraction, preparation and examination required by some other groups of smaller microfossils are not required. Despite certain difficulties attendant upon the use of ditch cuttings, quite adequate correlations can be made and the use of Foraminifera does not suffer from the disadvantage of requiring uncontaminated core as does the application of spores and pollen (palynology). The dramatic rise of Foraminifera as a major preoccupation of 'micropalaeontology' is therefore a reflection of the cost-effectiveness of their application in subsurface work dependent upon rotary drilling.

The chief difficulty that has to be faced in working with ditch cuttings is the strong possibility that the samples have been contaminated by geologically younger sediments caving off the side walls of the borehole during their ascent to the surface in the mud line. For this reason only the first appearances of index species can be relied on because there is no way of proving that further occurrences at lower depths are in place, rather than the result of caving. It is these 'tops', based on first appearance down the borehole (representing the last appearance in time), which are relied on for stratigraphical purposes in subsurface work. This procedure differs from that normal in surface work in which species can be traced from their first appearance in the strata through successively younger beds to their final extinction levels. Despite the disadvantage of this limitation to extinction levels (see further in chapter 14), effective correlation from well to well can be achieved by this means.

An example of the type of distribution chart usual in the oil industry is shown in figure 1.2. The species are plotted in order of appearance (with names of well-known index forms and numbers for local forms along the top). Only a semi-quantitative approach is possible with ditch cuttings, but it has been found useful to use symbols to distinguish relative frequencies in a unit sample, usually 100 g original weight.

The descending pattern of clustered symbols from left to right across the chart allows the tops to be selected on the basis of particular species and species groups. The intervals between important datum lines can then be distinguished as zones. The problem of caving is well brought out by the tendency of many species to recur at lower depths. In such cases, the complete absence of the species in question from cores taken at the same depth is very instructive. Fortunately, when conventional core is not available sufficient material for foram analysis can be obtained, in emergency, by the cheaper 'wire-line' method in which a small diameter, 1 in (25 mm), core tube is rotated on a line, or by 'side wall' coring in which a small tube is fired into the wall of the borehole by explosive.

Further difficulties include the possibility that samples may have taken longer than estimated from drilling times to reach the surface and that the tops are 'low'. This may be overcome by careful comparison of the results with the lithostratigraphy and especially with the geophysical logs which, as shown, may be conveniently included on the chart. The zonal

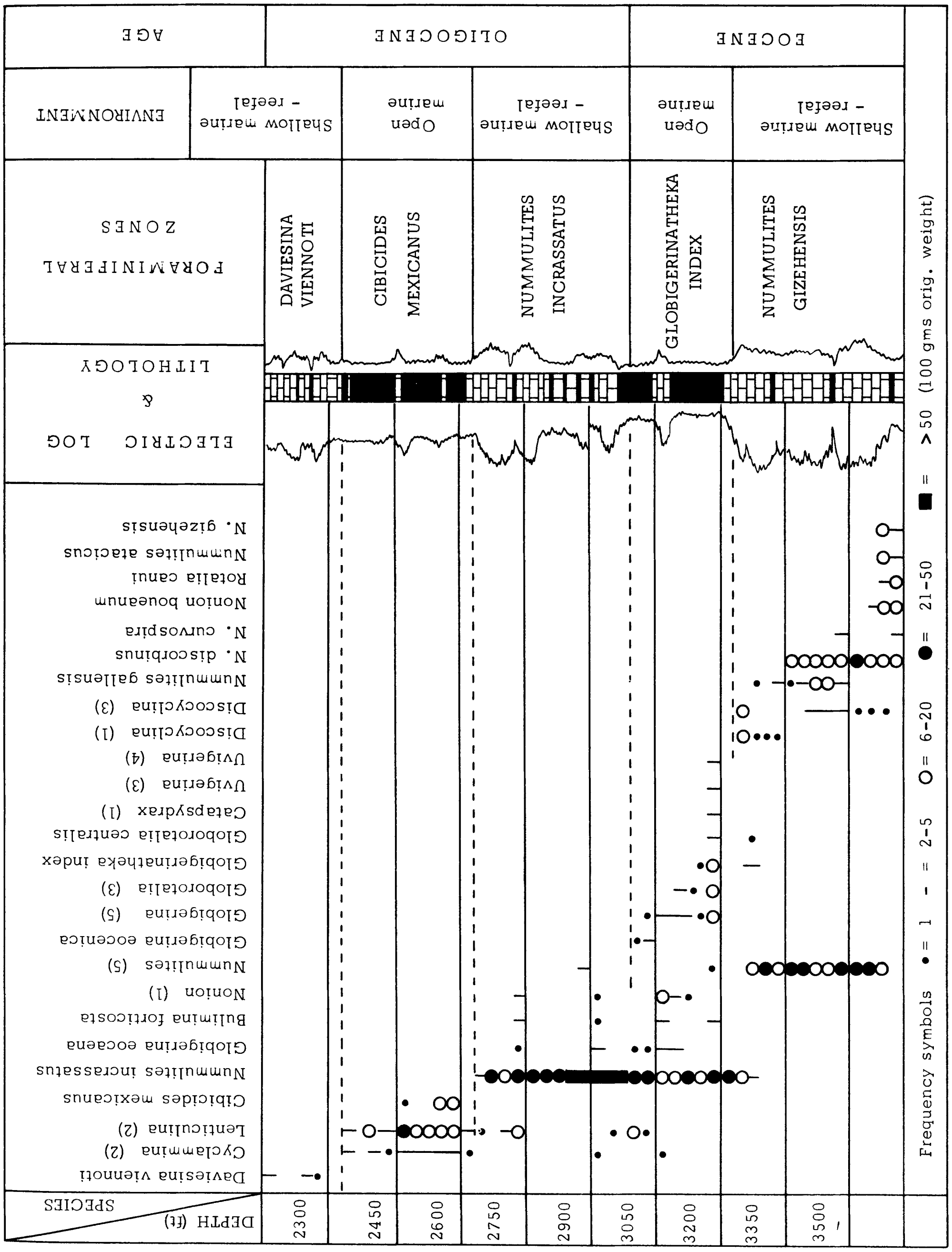

Figure 1.2 Distribution chart of Foraminifera in a subsurface borehole showing zones based on 'tops' in ditch cutting samples. Note that only a proportion of the index species are shown and the samples have been combined to represent 30 ft (9 m) intervals

stratigraphy and correlation with the standard stages, as well as the palaeo-ecological interpretation, is shown on the right-hand side. Evaluation of the oil prospects in a sedimentary basin generally requires study of several, strategically placed boreholes. The results can then be synthesised in a fence or panel diagram, as shown in figures 6.6 and 14.7.

It will be appreciated that as the deep sea drilling programme involves continuous coring, the problems of rotary drilling are not encountered and stratigraphical treatment of the samples is essentially the same as for surface samples.

In contrast to their position today, which is related to the economic imperatives of the twentieth century, the fame of forams in nineteenth century palaeontology was based largely upon the extraordinary abundance of Larger Foraminifera at certain stratigraphic levels (plates 1 and 3). On a number of occasions during the long evolutionary history of the group, relative giants of macroscopic size have arisen in a number of separate families widely separated in time. Some of these species were so successful, probably through exploiting the possibilities of a *symbiotic* mode of life in association with unicellular algae, that their dead shells built up massive limestones. This occurred particularly in the Upper Palaeozoic (fusulines), in the Upper Cretaceous (orbitoids), and in the Tertiary (nummulites, alveolines and lepidocyclines). Limestones consisting almost entirely of *Nummulites* are characteristic of the Eocene and Oligocene in the Mediterranean area of the former Tethyan seaway.

The Sphinx and the pyramids of Gizeh are all built from blocks of limestone from Mokattam in Egypt which consists almost entirely of one species, *Nummulites gizehensis* (plate 1). This genus was called *Nummulites* by Lamarck because of its resemblance to a coin (nummulus), while the trivial name indicates its provenance from the locality of Gizeh. This species was one of the largest foraminifers that ever existed and some specimens reach 7 cm in diameter. It was probably also the first known to man, as specimens were seen by the Greek historian Herodotus in his travels in the fifth century B.C. and were identified by Strabo as the petrified remains of lentils, provided by the Pharaohs as a food supply for the slaves employed in building their tombs.

Larger Foraminifera like *Nummulites* require the warm, sunlit waters of shallow, tropical and sub-tropical seas to live successfully. Similarly, most small, benthonic species (plate 2B) are acutely sensitive to facies control, including the factors of temperature, salinity, substrate and food supply. This means that the presence of extant species or related forms of fossils in stratified rocks is an extremely useful key to their environment of deposition.

A number of families of Foraminifera are abundant in the *plankton* of the pelagic realm in the open ocean. Many species are cosmopolitan and occur in broad latitudinal belts generally related to the temperature and the major ocean current systems.

Some species of *Globigerina* are so abundant that their dead shells make up a large proportion of the deep ocean 'ooze' (plate 2A). Almost a half of the abyssal plain beyond the continental shelves is covered with 'Globigerina ooze' which makes these Foraminifera the dominant rock-builders of recent time. In the North Atlantic the ooze is about 75 per cent Foraminifera and 25 per cent coccoliths (button-like plates of marine algae). To some extent it resembles the Chalk which represents a time in the geological past, at the height of the Cretaceous marine transgressions, when oceanic conditions of sedimentation invaded the continental shelves. However, the relative percentages of the two main groups are reversed in the Chalk and it is the coccoliths that dominate.

Planktonic Foraminifera show continuous evolutionary development from Cretaceous times. This, together with their wide distribution and independence of bottom conditions, makes them excellent index fossils. During the last two decades the attention of stratigraphers has increasingly turned to this group, especially after T. Grimsdale (former Chief Palaeontologist, Shell Oil Co.) outlined their possibilities for inter-regional correlation (Grimsdale, 1951). Eventually, W. Blow of British Petroleum Co. was able to erect 41 worldwide zones for the Cenozoic on the basis of these so-called 'ammonites of the Tertiary' (Blow, 1969). Figure 1.3 gives a version of this scheme taken from Saito, Burckle and Hays (1974). Incidentally, the history of the application of the planktonic Foraminifera in stratigraphy aptly illustrates the spur that economic use gives to foraminiferal studies.

SUMMARY OF THE REASONS FOR THE PARTICULAR VALUE OF FORAMINIFERA IN STRATIGRAPHY

(1) They are extremely abundant in most marine sediments, particularly in outer-shelf muds where several thousand specimens representing some fifty species frequently occur in a 10 ml volume

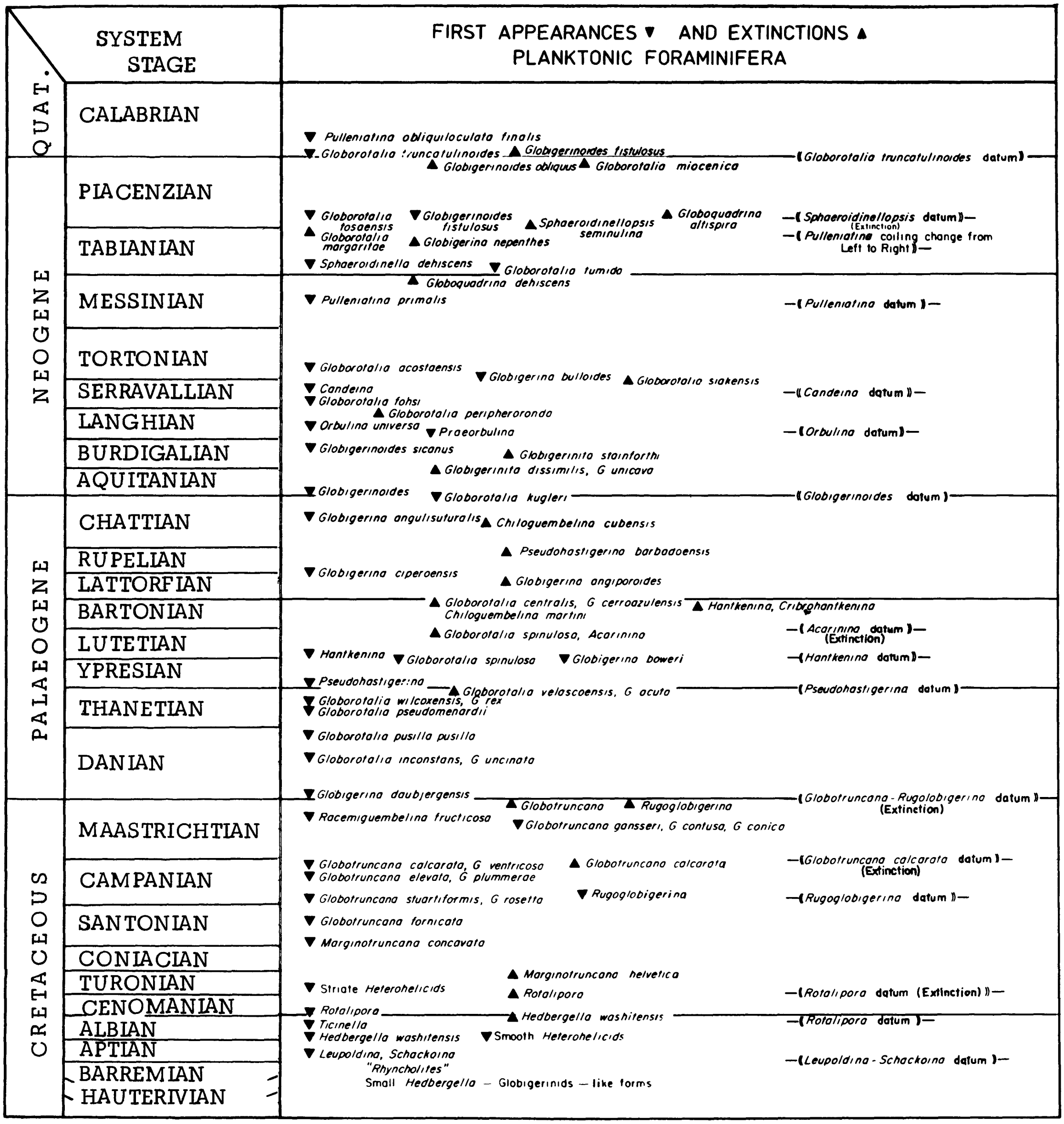
SYSTEM
STAGE
FIRST APPEARANCES ▼ AND EXTINCTIONS ▲
PLANKTONIC FORAMINIFERA
QUAT.
CALABRIAN
NEOGENE
PIACENZIAN
TABIANIAN
MESSINIAN
TORTONIAN
SERRAVALLIAN
LANGHIAN
BURDIGALIAN
AQUITANIAN
PALAEOGENE
CHATTIAN
RUPELIAN
LATTORFIAN
BARTONIAN
LUTETIAN
YPRESIAN
THANETIAN
DANIAN
CRETACEOUS
MAASTRICHTIAN
CAMPANIAN
SANTONIAN
CONIACIAN
TURONIAN
CENOMANIAN
ALBIAN
APTIAN
BARREMIAN
HAUTERIVIAN
▼ Pulleniatina obliquiloculata finalis
▼ Globorotalia truncatulinoides ▲ Globigerinoides fistulosus
▲ Globigerinoides obliquus ▲ Globorotalia miocenica
(Globorotalia truncatulinoides datum)
▼ Globorotalia tosaensis
▼ Globigerinoides fistulosus
▲ Sphaeroidinellopsis seminulina
▲ Globoquadrina altispira
▲ Globorotalia margaritae
▲ Globigerina nepenthes
—(Sphaeroidinellopsis datum)— (Extinction)
—(Pulleniatina coiling change from Left to Right)—
▼ Sphaeroidinella dehiscens
▼ Globorotalia tumida
▲ Globoquadrina dehiscens
▼ Pulleniatina primalis
—(Pulleniatina datum)—
▼ Globorotalia acostaensis
▼ Globigerina bulloides
▲ Globorotalia siakensis
▼ Candeina
—(Candeina datum)—
▼ Globorotalia fohsi
▲ Globorotalia peripheroronda
▼ Orbulina universa
▼ Praeorbulina
—(Orbulina datum)—
▼ Globigerinoides sicanus
▲ Globigerinita stainforthi
▲ Globigerinita dissimilis, G unicava
▼ Globigerinoides
▼ Globorotalia kugleri
(Globigerinoides datum)
▼ Globigerina angulisuturalis
▲ Chiloguembelina cubensis
▲ Pseudohastigerina barbadoensis
▼ Globigerina ciperoensis
▲ Globigerina angiporoides
▲ Globorotalia centralis, G cerroazulensis
Chiloguembelina martini
▲ Hantkenina, Cribrohantkenina
▲ Globorotalia spinulosa, Acarinina
—(Acarinina datum)— (Extinction)
▼ Hantkenina
▼ Globorotalia spinulosa
▼ Globigerina boweri
—(Hantkenina datum)—
▼ Pseudohastigerina
▲ Globorotalia velascoensis, G acuta
(Pseudohastigerina datum)
▼ Globorotalia wilcoxensis, G rex
▼ Globorotalia pseudomenardii
▼ Globorotalia pusilla pusilla
▼ Globorotalia inconstans, G uncinata
▼ Globigerina daubjergensis
▲ Globotruncana
▲ Rugoglobigerina
(Globotruncana - Rugolobigerina datum) (Extinction)
▼ Racemiguembelina fructicosa
▼ Globotruncana gansseri, G contusa, G conica
▼ Globotruncana calcarata, G ventricosa
▲ Globotruncana calcarata
—(Globotruncana calcarata datum)— (Extinction)
▼ Globotruncana elevata, G plummerae
▼ Globotruncana stuartiformis, G rosetta
▼ Rugoglobigerina
—(Rugoglobigerina datum)—
▼ Globotruncana fornicata
▼ Marginotruncana concavata
▲ Marginotruncana helvetica
▼ Striate Heterohelicids
▲ Rotalipora
—(Rotalipora datum (Extinction))—
▼ Rotalipora
▲ Hedbergella washitensis
—(Rotalipora datum)—
▼ Ticinella
▼ Hedbergella washitensis
▼ Smooth Heterohelicids
▼ Leupoldina, Schackoina
"Rhyncholites"
Small Hedbergella — Globigerinids — like forms
—(Leupoldina - Schackoina datum)—

Figure 1.3 Datum levels in the Cretaceous and Cenozoic based on appearances (inverted triangles) and extinctions (upright triangles) of planktonic Foraminifera. From Saito, Burckle and Hays (1974)

sample. According to Levine (1962) they constitute 2½ per cent of the animal kingdom and more than half the known protozoa. A number of species belonging to different families also occur in brackish water but only members of the non-testate Allogromiida occur in freshwater, apart from the anomalous occurrence of *euryhaline* species in freshened areas of the River Plate (Boltovskoy and Lena, 1971). Normally, therefore, the occurrence of Foraminifera is an indication of marine (high marine to brackish) conditions.

(2) They average about 0.33 mm in diameter (fine sand on the Wentworth scale), with a general range from 0.10 mm to 1.00 mm. This means that they escape destruction during the ordinary process of rotary drilling. They are easily extracted, filed for future reference and readily identified by means of the cheap, wide-field, stereoscopic binocular microscope. Elaborate and expensive techniques are generally not required. (See chapter 2.)

(3) Stratigraphic markers, 'tops', based on the first appearance of species and assemblages in

ditch cuttings can be applied in correlation which can be carried out without expensive coring.

(4) The sub-class has existed in abundance since the Cambrian, showing well-marked evolutionary changes useful in stratigraphy. Different families mark the Eras and major time Periods. (See sections on stratigraphical use in chapters 6 – 14.)

(5) Many species are planktonic and of worldwide occurrence in the broad latitudinal temperature belts. When this wide geographical range is combined with a short vertical time range they make excellent *(empirical) index fossils.* (See chapter 14.)

(6) Many species are restricted in their habit and narrowly confined to a particular ecological niche. They are thus particularly useful in interpreting the character of ancient environments. (See sections on ecology, chapters 6 – 14. Oxygen and carbon isotope analysis is also covered in chapter 14.)

(7) Many species, especially amongst the Larger Foraminifera, are so prolific that they are important rock-builders. Foram-limestones are well developed in the Upper Palaeozoic, the Upper Cretaceous and in the Cenozoic. (See chapters 7, 8 and 13.)

(8) Classification is based upon characters shown by the fossilisable test and therefore avoids the difficulties faced in those groups where a knowledge of the soft parts is necessary, difficulties which become acute in the case of extinct families. (See chapter 5.)

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Chapter 2

Collection, Preparation and Examination

> Numerous samples collected without a clear idea of what is to be done with the data are commonly less useful than a moderate number of samples collected in accordance with a specific design.
>
> (Krumbein, 1965)

Foraminifera occur on a wide variety of substrates at all depths in the marine realm and because their tests are generally of sand size they are also commonly transported by currents before burial in the sediment. They are therefore found fossilised in most types of sedimentary rock, particularly in clays and marls. Foraminifera are usually scarce in coarse sands but they are often abundant in silts and fine sands, especially if glauconitic. Many limestones are built up of Foraminifera but are often too hard or altered, as in the case of dolomites, to yield them by ordinary disaggregation techniques. They can then only be studied in thin section. In some cases the foraminiferal tests are silicified and may occur in the 'flint meal' of hollow flints in limestone, as in the well-known flints from the Upper Cretaceous chalk of Sonning in Berkshire. Derived silicified Foraminifera also occur concentrated in the basal 'Bullhead Bed' of the Thanet Sands where it overlies the chalk of the Upper Cretaceous Campanian stage in Kent.

FIELD SAMPLING

Normally, smaller Foraminifera are only rarely seen in hand specimens of rock samples in the field, so the only guide to their presence will be the lithology and perhaps the presence of an abundant calcareous macrofauna which will indicate former environmental conditions favourable to abundant marine life. Larger Foraminifera can be collected in the field like other macroscopic invertebrate fossils. Where they make up most of the volume of the rock, as is often the case with fusulines, alveolinids and nummulites, then they are easily observed in fresh exposures of the rock. They may also be observed in relief on weathered surfaces as well as on bedding and joint planes. Large Foraminifera may also be picked up or sieved out of sediment on talus slopes, particularly from the down wash on sea cliffs or scarps in arid regions where there is little cover of vegetation. A good example in the UK is the abundant occurrence of *Nummulites laevigatus* (up to 1 cm diameter) in talus at the foot of exposures of the Bracklesham Beds in Whitecliff Bay on the Isle of Wight. *Nummulites gizehensis* is so abundant in the Middle Eocene of the Sahara that at some localities it can literally be collected with a shovel. These are unusual occurrences, however, and the micropalaeontologist usually has to make a careful appraisal of the terrain in order that outcrops can be sampled economically but with the maximum possibility of obtaining fruitful material.

The density of sample coverage depends on the purpose of the investigation. When an oil company begins exploration of a new, little known area, field mapping and section measuring is carried out together with palaeontological dating, in order to establish the stratigraphical sequence. The emphasis is on section measuring rather than routine outcrop mapping, because the chief interest is in the thickness and character of possible source and reservoir rocks. It is also necessary to establish criteria for the recognition and dating of the rocks likely to be encountered in the subsurface during the course of drilling the favourable structures indicated by geophysics.

The micropalaeontologist should consider himself part of the exploration team and make every effort to accompany the field parties as often as possible. In this way he not only becomes familiar with the stratigraphical sequence rather than learning about it from second hand, which makes all the difference in stratigraphical evaluation, but is able to personally supervise the collection of samples for dating. The field geologists, as might be expected, tend to confine their attention to the possible reservoir rocks and as every commercial micropalaeontologist knows to his cost, will turn up at the micropalaeontological laboratory with requests for 'a date' on large, intractable lumps of crystalline limestone or even sucrosic dolomite! If the micropalaeontologist is a member of the field party, then as well as examining all rock types as far as practicable, special care can be taken to sample the finer clastics such as the clays and marls in which Foraminifera are often very abundant. A special effort should be made to search out clay partings between fossiliferous hard bands. In this connection, a former colleague developed a hooked device from a wire coat-hanger to pull out fragments of shale deeply recessed between limestone bands.

Commercial field work is usually severely limited by shortage of time and by the necessity to cover hundreds or even thousands of metres of vertical section in a season. So it may only be possible to sample each major lithological unit, say each member of a particular formation. But the effort should be made to take spot samples at approximately 10 ft (3 m) intervals, with combined or 'channel' samples through units considered important, with additional spot samples of shale-breaks and at particularly important horizons. This will give a coverage equal to the standard 10 ft intervals sampled in subsurface work and also enable the micropalaeontologist to go beyond simple dating to give some consideration to the palaeo-ecological relationships of the fauna and the environment of deposition. This will enable him to play his part in the full geological interpretation of the strata which is so important for the prediction of stratigraphical oil traps as well as for knowledge of the origin and time of migration of the oil. He may find that his colleagues need to be educated in the possibilities of micropalaeontology in this regard, and he should strongly resist any tendency to become stereotyped as merely the expert on biostratigraphical dating, which tends to happen as easily in large commercial concerns as in bureaucratic government research centres. There is no doubt that much of the potential of foraminiferal studies is lost in such an event.

Academic studies do not normally suffer the same constraints as commercial work and the strata can be more closely sampled. Attention may be confined to one formation only which can be fully covered, with channel samples taken bed by bed as well as spot samples taken at the bottom, middle and top of beds. Comparative samples can also be taken from equivalent sections down-dip or along the strike so that a full facies analysis can be undertaken. Where variation and evolutionary studies are being made it may be necessary to sample inch by inch or centimetre by centimetre depending on the degree of resolution required.

About 250 g weight of sample is usually considered sufficient for analysis, so about 500 g should be collected to give an adequate reserve.

While collecting, it is important to avoid contamination. Picks, shovels and trowels should be carefully cleaned and rock samples should be brushed over before bagging and later washed and scraped before preparation if necessary. Samples should be collected in thick-gauge plastic bags, or linen bags which are to be preferred for hand specimens of sharp-edged limestone and sandstone and have the advantage of attached labels and ties. Sample bags should be numbered on the outside and a duplicate label, with numbers in waterproof ink, placed inside. All 'float' samples collected from talus, etc., must be clearly indicated. Where the samples are collected as part of a field mapping survey, the numbers and localities are entered into a field notebook and plotted later on a base map. When collection proceeds together with detailed section measuring, a graphic lithological log should be drawn to accompany the detailed description with the position of the samples shown exactly. If possible, polaroid photographs should be taken of the section with sample bags (or marker flags) in position. Junctions can be drawn and explanations written on immediately in white ink. In many oil companies the field notebooks are company property and are eventually stored in the company library, while one base map records the sampling of all field parties. The notebook therefore has to be written up in a clear, explicit, logical manner so that it can be easily understood by other workers and leaving nothing to memory. The micropalaeontologist should adopt this approach as a matter of course.

Samples from Borings

As was explained in chapter 1, the majority of oil wells are drilled by the rotary drill and the cuttings are carried out by the drilling mud to be caught in a mechanical sieve, 'shale shaker'.

Samples representing each 10 ft (3 m) interval are usually taken, normally about half a kilo. The drilling mud is washed off and the material split into subsamples of approximately 100 g weight, and stored in plastic or linen bags marked with well name and sample interval. The subsamples are needed not only for micropalaeontological and sedimentological research but because it is common practice for companies to swap runs of samples with competitors. The enormous number of bags that eventually come into the oil company warehouse from wells that may be over 10 000 ft (3 km) deep, together with boxes of core as well as field samples, make detailed accounting and documentation necessary. The micropalaeontologist is usually in charge of this material and a card file is kept to aid location and retrieval.

Cores, when properly cleaned of drilling mud, yield the best samples for foraminiferal analysis because the depth at which the sample is taken is accurately known and the material is uncontaminated. It is best to sample continuously through each lithological unit present in the core. Cores are usually boxed in 3 ft (1 m) or 5 ft (1.5 m) lengths, so a separate channel sample can be taken with a chisel along each length. In addition, spot samples can be taken at important horizons, as of shale breaks in sandstone or limestone. These samples are hammered or chiselled transversely off the core and slices about 1 cm thick are generally taken.

Samples taken at Sea

Cores of solid rock taken during marine geological surveys are treated in the same way as cores taken on shore, but cores and 'grab' samples of incoherent Recent sediments present a different problem. Cores taken by simple gravity corer, such as that of Phleger (1960), or by the Multiple Corer of Barnett and Watson (plate 4, no. 4) which is lowered to the sea bed to take an undisturbed sample, are recovered in a plastic tube. In this case subsamples are taken immediately on board the research vessel. The core is gently extruded by means of a cork on the end of a rod which allows 1 cm slices to be cut off in succession. These are placed for storage in plastic tubs with addition of 5 – 10 per cent formalin to prevent decay of the microfauna which are live at the time of collection. It is advisable to buffer the solution with borax at 10 g/l to counter undue acidity which could lead to dissolution of calcareous shells. Large cores taken by the Box Corer (Gage, 1977; cf. Hessler and Jumar, 1974) can be conveniently subsampled by inserting a small plastic tube which is then extruded for slicing.

Samples taken by a grab such as the 'Shipek', or from the bucket attached to the dredges used in macrofaunal surveys, are preserved in the same way. In this case the cut sediment is placed in a plastic tub, not more than half-filled, and left just covered with sea water which is then topped up with buffered formalin. Care should be taken to label the lid on the inside and the outside, as well as the tub, with the station number. When only cobbles and boulders are recovered by the grab these can be preserved intact if small enough, otherwise the epiflora and epifauna should be scraped off and preserved for later examination of the attached Foraminifera.

It is important to stress here that sampling should be carried out as part of a general marine survey, with side-scan sonar and subsea TV, so that samples can be taken of various substrates and material recovered representing as many micro-environmental niches as possible.

The location of the sample station and details of sediment character, associated macrofauna and flora, etc., are entered in a log book immediately upon sample recovery. The samples can be plotted on a base chart and the details transferred to reference cards on arrival of the samples at the shore-based laboratory.

SAMPLE PREPARATION

The different rocks containing Foraminifera require different methods of treatment, but as a rule the less rough treatment the samples receive the better; they will be less damaged and broken when recovered. The general procedure is as follows:

(1) *Crushing and boiling*. The sample is dried, either in the air or in an oven, and a subsample of a definite weight is soaked in water—if possible, not more than half the original sample so that ample material is left for future reference.

Some very soft, friable rocks including shales, marls and sands, particularly from the Cenozoic, may break down on soaking for an hour or two, but harder rocks first require crushing in a vice. Care must be taken that the rock is not broken into fragments smaller than the largest Foraminifera present, say 1 cm diameter, which is the average size of rotary cuttings. The sample from the Lower Lias of the Mochras Borehole, shown being weighed out in plate 5, no. 1, has been crushed to a smaller size because the Foraminifera are all very small at this horizon. The broken rock may then be soaked in water. This may be sufficient to bring about disaggregation, but normally slow boiling for an hour or more with washing soda (sodium bicarbonate) at 50 g/l, or a spoonful of a sudsless detergent such as Alconox, is necessary to produce clean specimens. Plate 5, no. 2, shows the sample of crushed Liassic shale being boiled in a saucepan over a bunsen burner. Enamel saucepans are easier to handle than glass beakers and are used in preference to stainless steel or aluminium ones which tend to become pitted very rapidly. They are used until the enamel begins to crack off and are then thrown away.

(2) *Decanting*. As the mud goes into suspension during boiling it is poured off, half the volume of liquid at one time, the pans being topped up with fresh water until the residue is clean. To avoid loss of specimens this should be done through a fine mesh sieve (B.S. 240 mesh with openings of 63 μm will retain smaller Foraminifera and most of the juveniles) after cold water has been added to lower the temperature, as in plate 5, no. 3. The residue is finally poured into the sieve and the finer material flushed gently away with a spray nozzle.

(3) *Drying*. The residue can be dried, still in the sieve, under an infrared lamp or in a drying oven (plate 5, no. 2). Alternatively the residue can be flushed from the sieve into a filter paper in a glass funnel (plate 5, no. 3). The filter paper can be turned over and secured with a paperclip and the sample again oven dried or, as in the U.C.W. laboratories, dried over the bench radiator grilles at room temperature.

(4) *Storage*. If the sample is to be studied fairly soon it can be left in the filter paper, otherwise it must be transferred to a plastic or glass vial for safe storage.

It is important to adopt a clear system of labelling with numbers or letters that accompany the sample through the washing and drying process (plate 5, no. 3). The storage vial should be labelled outside and a paper label should also be placed inside.

ALTERNATIVE METHODS

Where the sediment proves difficult to disaggregate, all that may be necessary is to repeat the boiling procedure after the residue has been dried. In many cases the mud or shale pellets will then break down. Highly indurated shales may, however, require alternative methods. One technique that is often successful with bituminous or carbonaceous shales is the use of paraffin or white spirit as a solvent. The sample is dried and soaked in white spirit overnight. Excess white spirit is then poured off and hot water with Alconox or washing soda poured on, followed by the normal washing procedure. This method was discovered by one of the French oil companies drilling in the Sahara—it was noticed that hard dark shales outcropping near the drilling platform were breaking down after being soaked in waste petroleum.

Some shales will break down if first soaked in dilute hydrogen peroxide (15 per cent). The process is speeded up if the sample is hot, but the oxidation reaction is violent and care must also be taken with pyritous shales as the reaction may damage and even destroy the pyrite-filled tests as this mineral is converted to iron oxide.

It may be found that some sediments break down quite well initially but reduce to clay pellets that prove very difficult to disaggregate further. Such sediments often break down completely if transferred in a beaker of hot water to an ultrasonic vibrator for 1 – 2 sec treatment. Only part of the residue should be treated at a time in case of breakage of the foraminiferal tests. The same treatment can be used for specimens such as planktonic species from ooze that have sediment adhering to the test and hiding important features.

Other methods which have been found successful in certain instances include:

(1) Use of a rolling mill. The sediment is rolled in screw-top glass jars, each with a rubber-covered lead slug inside, hot water and washing soda being added.

(2) Use of a kitchen mixer with hot sudsy water. The mixer bursts the shale fragments and the freed Foraminifera float up in the suds. The Foraminifera are often broken, but if the sample cannot be broken down by any other means this is still worth while.

(3) Pressure cooking.

(4) Freezing and thawing.

(5) By soaking in hypo with growth of crystals within the rock.

(6) By soaking in bromine.

Treatment of Recent Sediment Samples

Recent samples can be washed with cold water but require staining so that Foraminifera which are live at the time of collection can be detected. The procedure is as follows:

(1) A 10 ml cut is washed clean of mud and preservative under a fine spray of water over a fine mesh screen (B.S. 240 with openings of 63 μm). The volume of the cut can be measured in a graduated vial.

(2) The sieve containing the washed residue is

placed in a bowl of Rose Bengal stain (at 1 g/l) so that the solution well covers the sediment on the screen. Staining is allowed to proceed for 20 min with occasional shaking. In most cases this leads to pronounced red staining of contained protoplasm, although opaque species may have to be broken for this to be seen.

(3) The residue is washed under a fine spray of water to remove stain from the sediment and from the shell walls of the Foraminifera. It can then be examined wet in a petri dish (this is advisable in the case of material containing fragile membranous and agglutinating species), or alternatively flushed out of the sieve on to filter paper in a funnel where it is left to dry in the air. The filter paper can then be secured with a clip until examination or the sample stored in a standard 10 ml vial. An alternative staining method, using Sudan Black, which may give better results in certain circumstances but is more complicated to apply, is given by Walker, Linton and Schafer (1974).

Separation of Foraminifera from Limestones

Recovery of microfossils from limestones is more difficult than from the softer clastics. However, chalks and the softer marly and more crumbly limestones may be crushed and boiled with successful release of microfossils. This is particularly the case where the grain size is the same as that of the fossils, as in some fragmental limestones whole Foraminifera and ostracods will then break out. The Middle East Tertiary limestones are often highly foraminiferal and in most cases crushing and boiling release a good percentage of the fauna. Where fossils remain partly embedded in the limestone it is often possible to dig them out with a needle or break them out with a vibro-tool.

Membranous and arenaceous Foraminifera may be recovered from limestone by leaching with 10 per cent HCl or 5 – 50 per cent acetic acid. The rock specimen is immersed in the acid and when effervescence ceases more is added until no more effervescence occurs. The sample is then washed and dried very carefully, as the residue is usually very brittle. Results may be spectacular where the Foraminifera are silicified.

THIN SECTIONS

Foraminifera in hard dense limestones must be studied in thin sections made in the following way:

(1) By use of a diamond saw, cut a parallel-sided slice about 3 cm long by 2 cm wide by 5 mm thick.

(2) Surface the slice by grinding with 80 grade carborundum on an iron plate.

(3) Wash and transfer to a glass plate and grind with very fine carborundum.

(4) Cement the prepared surface to a glass slide with Canada balsam or Lakeside. The slide should be ground for better adherence. Heat the balsam to the necessary hardness on a hot plate—when a thread drawn out with forceps snaps at a touch. Mount specimen after slight reheating of the balsam, a drop of balsam being put on the slice as well as on the slide.

(5) Grind the other side of the slice in successive grades of carborundum until the required thinness is attained, and the fauna can be seen under the microscope.

(6) Warm the slide (when cleaned) to 100°C. Place a drop of balsam on a coverslip and place over the specimen.

Separating Foraminifera from Washed Residues

After the sample has been successfully washed down and dried, the residue of sand and mineral grains is sieved into fractions for ease of examination by reflected light under the binocular microscope. Brass sieves of a convenient size (100 mm diameter) are shown in plate 5, no. 5. Mesh sizes of B.S. 60 mesh, aperture 250 μm, and B.S. 100 mesh, aperture 150 μm are generally used and the finest fraction, +63 μm, is caught in a receiver. Most of the Foraminifera are generally found in the 60 and 100 mesh fractions but may on occasion, as in the case of the Liassic Foraminifera from Mochras, be concentrated in the fines which also tend to include the juveniles. Large Foraminifera will be retained on the 30 mesh sieve, aperture 500 μm. It is therefore necessary to look at all the fractions. Attention should not be solely confined to the 30 and 60 mesh, as was often the case in earlier times and is still sometimes practised by commercial concerns for 'economic reasons'.

The residue is tapped gently out of the sieve on to a small tray of metal or black card so that the grains are evenly spread and not on top of one another. Avoid the beginner's mistake of piling the material in heaps under the impression that this will speed up examination, as it makes it impossible to see and separate all the microfauna.

A useful tray of smooth, matt black 'scratch board' is shown in plate 5, no. 5. This has raised sides of gummed card, to prevent specimens rolling off, with a small space at one corner for brushing the residue into a storage vial after examination. The tray is marked out in squares of approximately the area of the field of the binocular microscope and at a convenient magnification for general appraisal of the residue, about × 25. This allows all the residue on the tray to be looked over systematically.

The Foraminifera are picked up by means of a moistened artist's brush of 00 or 000 size and transferred to a cavity slide where they can be preserved loose for later examination. A 'three-hole' cavity slide of punched white card with a matt black scratch board base and coverglass held by gummed tape is shown in plate 5, no. 5. This type of slide allows the Foraminifera from the different fractions to be kept separate, which may be important for evidence of mechanical sorting in death assemblages. 'One-hole' slides are used for type and representative specimens, while rectangular cavity slides with a grid of white painted squares (5 to 100) are used to mount representative faunas, the individual specimens being stuck down with gum tragacanth or water-soluble plastic.

Most of these types of slide are manufactured commercially but often have fibrous black card as a base and plastic coverslips which become charged with static electricity and attract the specimens which may then be lost or crushed. They can easily be made in the laboratory with simple equipment including a punch to cut out circular holes, as in plate 5, no. 4.

The slide is made from a strip of white card 75 mm long by 25 mm wide and up to 3 mm thick. One to three holes of 14 mm diameter are punched out, or a rectangular cavity cut with a scalpel, and the slide is glued to a base of matt black scratch board. Up to ten can be made at a time and they can then be held all together in a vice to prevent warping while the glue sets. The sleeve is made from a thin glass microscope slide, to which strips of gummed tape are attached. These strips fold over to hold the base of the sleeve, which is made from thin white card with 'thumb holes' cut from each end to facilitate pushing out the cavity slide. The grid for the faunal slide can be made from the negative photograph of an indian ink drawing suitably reduced, which has the advantage that the emulsion will hold small Foraminifera when mounted with a wet brush. Care must be taken to cut the card precisely so that the slides will fit the trays in metal or wooden cabinets specially manufactured for their storage. The wooden slide cabinets illustrated in plate 5, no. 1 hold some 900 slides on trays, with three divisions each holding 12 slides (plate 5, no. 4). These cabinets have the advantage that they can be stacked as units on top of one another.

Use of Heavy Liquids

A liquid of high density such as carbon tetrachloride or bromoform can be poured on to the dried residue in order to float off the relatively light, air-filled Foraminifera which can then be caught on a filter paper in a glass funnel. This method has the disadvantage that infilled specimens and agglutinating forms may not float and the results are often quite variable. For quantitative work the residue must still be diligently searched, so two operations become necessary and time may not be saved. It is chiefly valuable as a way of concentrating specimens from large amounts of residue when strictly quantitative methods are not called for—see, however, Carlton (1933). When using heavy liquids the student must take care to carry out the operation under a fume-hood, as inhalation of the fumes is dangerous.

Sorting, Further Preparation and Identification

The experienced worker may recognise most of the genera and many of the species present in the residues, and be able to pick them out and mount them immediately on faunal grid slides. Otherwise, all the samples from the particular section under investigation should be picked and specimens compared before the species are identified and representative specimens are mounted for future reference on one-hole slides (for the principles of classification and description of new species, see chapter 5). These slides, unlike faunal grid slides, have the advantage that the name and full locality and samples details can be written on them. They *must* be used for new species so that after the publication of a formal description they can be safely deposited in a museum collection. A selection of specimens should be mounted, to show the full range of variation, on a separate slide from the 'type' in the case of new species.

In commercial work, study of rotary cuttings begins from the top downwards (see chapter 1), and there is usually pressure for information before the worker has looked at all the samples, but here too selection of representative specimens of new species and species occurring for the first time in the area should be delayed until a range of samples from the particular zone has been examined. It is common practice to give numbers provisionally to species which cannot be readily identified, but identification should be carried out as soon as possible so that the full stratigraphical and ecological value of each species is realised.

Details of the external structure may be shown more clearly if the specimen is stained with malachite green, methylene blue or even green ink. Normally, careful examination under the optical microscope is sufficient to establish specific distinctions and the results are quite adequate for application in stratigraphical research and commercial work. But, the description of new species and redescription of old-established ones may require examination of the very fine details (ultrastructure) of the wall, ornament, perforation and apertural form and recourse to the scanning electron microscope. The Cambridge Instruments model S600 is shown in operation in plate 6, no. 1. In this microscope the specimen is scanned by a narrow beam of electrons (width about 100 Å) focused through a series of magnets, and the differential return of secondary electrons and reflected primary electrons builds up a picture on a screen. Advantages are the high resolution down to 200 Å, considerable depth of field, hundreds of times greater than the optical microscope, and possible magnifications to over ×20 000. A further advantage is the working distance of about 3 cm between the specimen and the electron collector (Oatley, 1966; Paterson, 1965).

Preparation of specimens for examination by SEM is fairly simple compared to the replication process required for examination of specimens by transmission electron microscope (TEM):

(1) Carefully clean specimen, particularly of gum tragacanth, and dry off with 80 per cent alchohol mixed with methanol.

(2) Mount on aluminium stub with wax, 'dag' (a suspension of silver in alchohol), double-sided transparent adhesive tape, or Kodaflat.

(3) Plate with gold or aluminium evaporated under vacuum.

An even and complete metal coating is required together with secure mounting to prevent build-up of electrons in the specimen and charging effects.

A disadvantage of examination by SEM is that, although it allows the mapping of surface features in beautiful detail, internal features are obscured and smooth opaque specimens show less detail than by optical microscope.

The examination of opaque specimens by optical microscope is made easier if the specimen is wetted or removed to a hollow glass slide and immersed in a drop of xylene which acts as a clarifier, cutting down the reflected light. Fine details, including the arrangement of the chambers in the initial part, may now be seen, especially if the specimen is looked at in transmitted light. The advantage of the use of xylene is that it evaporates from the specimen after a short while, leaving it clean. For more prolonged study of internal characters, the specimen can be mounted in glycerine or castor oil (Hofker, 1951) or embedded permanently in Canada balsam or Lakeside 70.

Where internal details cannot be seen by these methods it may be possible to breach the external surface by use of dilute acid applied with a fine brush. Otherwise it will be necessary to make thin sections; these are obligatory in the case of the annular complex and fusiform Larger Foraminifera which generally require both equatorial (or median) and axial sections for identification.

Thin Sectioning of Individual Foraminiferal Tests

Sometimes only a half-section is required and a large specimen of a nummulite or orbitoid may be rubbed down on a fine hone with a slightly hollowed cork or even with the fingers until one-half of the specimen is worn away. Both axial and equatorial sections can be made in this way.

For the sectioning of Larger Foraminifera:

(1) Cement the specimen with balsam to a glass slide.

(2) Grind to the middle line or desired point with a ground glass slide.

(3) Warm the slide and turn the specimen over with a needle.

(4) Grind to the required thinness.

(5) Warm the slide. Place a drop of balsam on a coverslip and place over the specimen.

For the sectioning of Smaller Foraminifera, following the method of Wood (1948):

(1) Immerse the specimen in xylene with a little added Canada balsam in a hollow glass slide.

(2) Allow the xylene to evaporate naturally so that the balsam penetrates into the interior chambers of the test.

(3) Cement a celluloid or mica coverslip (2 cm square) to a glass slide.

(4) Place specimen on top of the slip in balsam and heat to the correct hardness.

(5) Grind down the specimen to the desired plane with the finest laevigated carborundum or with a ground glass slide.

(6) Wash and flake off the coverslip with the specimen attached.

(7) Remount the coverslip in clean balsam on a new glass slide, with the specimen now on the underside.

(8) When cold, flake off the coverslip leaving the specimen on the slide, 'upside down'.

(9) Grind the specimen to the required thinness.

(10) Wash then warm the slide. Place a drop of balsam on a coverslip and place over the specimen.

Use of the celluloid or mica slip ensures that the two sides of the section are parallel.

A method which avoids the problem of contamination by carborundum particles by the use of small grinding stones is given by Hofker (pers. comm.):

(1) Suspend the carborundum in dentist's cement.

(2) Harden in small boxes.

(3) Grind to a flat surface on a carborundum stone.

(4) Grind the embedded specimens on the prepared stone using *Rhicinus* oil.

(5) On completion, remove any extraneous grains by adding a drop of oil and lightly rubbing the surface.

(6) Remove the oil with paper tissue.

Special Techniques for Examining Internal Structures

Casts

Natural casts formed by infilling of the test with minerals such as pyrite sometimes reveal details of internal structure not seen externally. The making of artificial casts goes back to Carpenter, Parker and Jones (1862) and a method is described by Hofker (1927) who produced beautiful casts of Nummulitidae showing the internal canal system:

(1) Soak test in xylene.

(2) Cook in Canada balsam.

(3) Slightly grind and immerse in 5 per cent acetic acid for 24 h until decalcified.

Satisfactory impregnation of specimens to fill all the chambers and canals is difficult and to overcome this Hansen and Lykke-Anderson (1976) suggest the making of half-sections:

(1) Grind down the specimen which is embedded horizontally in Lakeside 70 on a glass slide to plane of proloculus.

(2) Reheat and turn over the specimen with a hot needle so that the section is in contact with the slide.

(3) Cool and remove excess cement with a pointed scalpel under the microscope. A thick layer of cement is required so that brittle splinters can be removed to expose the shell surface.

(4) Immerse in 10 per cent HCl for some minutes to decalcify.

(5) Wash in water and dry.

X-ray Microscopy

Sectioning and the making of casts leads to partial or complete destruction of the test. A method of revealing internal structures without damaging the specimen is by microradiography—either contact microradiography, where the specimen is placed in the path of the beam very close to the photographic plate, or by point projection microradiography, where the beam is focused on a metal target which emits the X-rays which then penetrate the specimen to produce an enlargement on a photographic plate (Hedley, 1957; Hooper, 1959).

The mineralogical constitution of the test is also best studied by the techniques of X-ray microscopy, employing X-ray diffraction equipment (Switzer and Boucot, 1955). Using the powder technique the X-ray beam is diffracted from the planes of the atoms in a crystal in patterns that reveal its form according to Bragg's law. This allows the recognition of the two main groups of calcareous Foraminifera—those composed of calcite, the hexagonal crystal form, and those composed of aragonite, the orthorhombic crystal form, to be distinguished. Using this technique a specimen can be X-rayed uncrushed, held at the end of a glass fibre.

A further development is the electron probe microanalyser (EPM) which focuses down to a spot about 1 μm in diameter and allows study of the variation in elements in different parts of the test (Hooper, 1964). For this technique the specimen must be embedded in epoxy resin or polystyrene and sectioned as for examination by SEM. The sections are then polished on rotating wet velvet discs with chromium oxide powder before being placed under the probe.

Special Techniques for Examining Wall Structure

Whole specimens can be examined as advised by Wood (1963):

(1) Clean the specimen and immerse it in absolute alchohol.
(2) Place in xylene in a hollow glass slide.
(3) Examine under the crossed nicols of a petrological microscope at ×100 with the condenser out, brightly lit and with the plane side of the mirror in use.

Alternatively the specimen may be crushed under a coverslip and the fragments examined or sections cut at right angles to the wall and septa.

Freshly broken surfaces and transverse sections made by the normal methods require special preparation for examination by the scanning electron microscope. To follow the method of Hansen and Lykke-Anderson (1976):

(1) Prepare the transverse section on a glass slide in Lakeside cement.
(2) Polish on a wet, velvet-covered disc with MgO powder or Al_2O_3 paste.
(3) Wash with oil-free detergent.
(4) Etch with aqueous EDTA solution buffered to pH 7.0 by NaOH for 15 – 60 sec according to wall thickness.
(5) Cut out the specimen from the slide with a glass cutting pencil to give an area small enough to mount with double-sided transparent adhesive tape on aluminium specimen stub.
(6) Plate with 250 – 500 Å gold under vacuum with two tungsten filaments rotating at 5° and 45° angles of evaporation.

For studying the surfaces of fractured specimens, Bellemo (1974a) has used the following method:

(1) Remove organic membranes with concentrated sodium hypochlorite.
(2) Etch crystalline elements with 25 per cent solution of glutaraldehyde buffered to pH 3.5 for 5 – 20 min.

The specimen is then mounted on an aluminium stub and plated with evaporated gold as above. If it is desired to examine the organic lamellae then the test can be demineralised with chromium sulphate solution, with immersion for 8 – 30 min.

The student must take great care in the interpretation of the results of these etching processes in order not to confuse artefacts of the technique with natural structures.

LITERATURE SEARCH

Identification of species requires careful comparison with published figures and descriptions in literature dealing with the area under investigation, or on strata of the same age in adjacent regions, and use of catalogues such as the McLean Card Catalogues and the Ellis and Messina Catalogue of Foraminifera, listed in the literature to chapter 1. In plate 5, no. 6 the Ellis and Messina Catalogue is shown arranged alphabetically by genus in suspension files which makes both consultation and addition of new species descriptions easy. Other catalogues such as the McLean series are stored in small cabinets above.

The vast literature on Foraminifera now makes the Ellis and Messina Catalogue practically obligatory for serious foraminiferal work. The problem is made more difficult because most descriptions and discussions of faunas are published in papers widely scattered in various learned journals. These papers are most easily dealt with as 'separates' or xerox copies. Some 6000 are stored in the Micropalaeontological Library of the University College of Wales under authors' names, in alphabetical order. As shown in plate 5, no. 6 they are kept in cardboard pamphlet boxes and retrieval is aided by a cross-reference system on small cards arranged by topic, stratigraphic system, family group, etc.

Consultation of the literature and comparison with specimens in museum collections is required not only to identify each species but to check all records in order to establish its full stratigraphical and geographical range. This information is entered on separate data sheets, together with details of the occurrence of the species in the sections and samples under investigation. Separate data sheets are also kept on each sample. These record:

(1) Sample number, location and collector.
(2) Horizon or depth in borehole.
(3) General character and lithology.
(4) Preparation techniques and amount treated.
(5) Residues examined.
(6) Associated fauna.
(7) Foram species and frequency.
(8) Age.
(9) Ecology.

This information can conveniently be entered on prepared form sheets with columns for the species names, frequencies in different fractions and, if necessary, an indication of whether the specimens were live or dead on collection. In ecological work, where the expected species are well known, the names can also be written into the form sheet in advance.

ILLUSTRATION

The literature search and comparison with descriptions and actual specimens of other species is made easier if figures have already been prepared to illustrate the characteristic features of the species under investigation. Care should also be taken to show variations that may be confined to the local population. A convenient way to do this is by a camera lucida attachment to the binocular microscope, as shown in plate 6, no. 4. Here the equipment is attached to the right-hand ocular of the microscope and consists essentially of a prism and a mirror which allow the image of the specimen seen through the microscope and that of the paper on the drawing board to be brought together. The outline of the specimen and other features may then be accurately traced out. As shown in the plate, the drawing board needs to be fixed at the angle of inclination of the oculars. Also, the lighting of specimen and drawing board has to be balanced so that the point of the pencil used can be clearly seen against the image of the specimen, achieved in this case by use of a fluorescent tube attached to the drawing board.

In the case of new species and redescription of established species, where the illustrations are intended for publication, the drawings should be done on good quality white card, such as Bristol board. They can be carried to completion with indian ink stipple shading or pencil shaded and cut out for mounting on matt black card, which gives the realistic effect of viewing the specimen down the microscope. The drawings should be prepared at a size which will allow reduction to half-size in the final publication.

In the recent past, illustration of Foraminifera by photomicrography, apart from thin sections, was beset by considerable difficulties caused by the limited resolution and depth of field of the optical microscope. The appearance of the SEM with its great range of magnification, high resolution and depth of field has made photomicrography of external details relatively easy, including the making of stereopairs. This method has now become standard. In plate 6, no. 1, a 35 mm camera can be seen mounted to the right of the display unit of the SEM; this allows a photograph to be taken of the image and simultaneously shown on the screen as well as the TV monitor. Photographs made by this means can be cut out and mounted on black card in the same way as pencil drawings (plate 6, no. 2). In this case there is no advantage to be gained by reduction so the plate can, with economy, be prepared at publication size. The individual figures can be labelled with stick-on letters.

Despite the success of photomicrography by means of the SEM, the student should not be led to the belief that light photomicrography is now quite redundant. There are a number of groups, particularly smooth, lamellar forms, which show little detail under the SEM. Better results may be achieved by light photomicrography if advantage is taken of the methods introduced by Fournier (1954, 1956), including the use of the pinhole diaphragm to increase the depth of field. The student should also note the excellent results of Albani (1964) using Zeiss Luminar lenses and bellows and universal stage for orientating the specimen. A modification of this system, developed by Dr D. Bates of the University College of Wales, is shown in plate 6, no. 3. Here, a polaroid film holder is attached to the bellows and the specimen, a foraminifer fixed to a scallop shell, is mounted on a simple microscope substage and lit from three sides by a flexible glass fibre intensity lamp. With the film holder removed and a ground glass screen in place on the bellows, the specimen can be brought into focus by movement of the stage. Photographs can be taken one at a time and the results examined immediately when using this equipment.

Photographs of the internal structures of opaque specimens and specimens with involute and embracing chambers can be made by X-ray microradiography. Results obtained by this means and details of apparatus can be found in Bé, Jongebloed and McIntyre (1969).

SUMMARY

Foraminifera occur in most sedimentary rocks but particularly in the finer clastics. Few can be observed in hand specimens, so collection must be systematic and planned according to the purpose of the investigation. Normally, the range of different rock types present should be sampled to allow a full stratigraphical appraisal. Sufficient material must be obtained to allow a reserve for future research and exchange. Great care must be taken to avoid contamination, to bag the samples securely and to provide full documentation. In particular, talus must never be included with *in situ* material. Detailed filing is necessary for retrieval of cuttings and core stored in company warehouses, and special care must be taken to preserve submarine cores and grab samples containing Foraminifera which are live at the time of collection.

Samples should be disaggregated in a manner that will maximise faunal recovery with least breakage of the tests. Simple washing should be tried before more elaborate methods are resorted to. Decanting should be done through a sieve with a mesh opening of 63 μm and the residue picked after sieving into fractions on mesh openings of 500, 250 and 125 μm. A clear, foolproof system of labelling should be followed throughout the whole washing, drying and picking process. Recent material requires staining with Rose Bengal or Sudan Black, and picking and counting should be done wet if fragile agglutinating species are present.

Highly indurated limestone and sandstone must be examined in sections cut by the normal petrological methods, while special techniques are required for sections of individual foraminiferal tests and for preparation of sections for examination by TEM or SEM.

Picked material can be sorted on simple cavity slides made in the laboratory, and 'three-hole' slides are especially useful for the study of size sorting. Selection of type specimens of new species should be delayed until a range of material has been sorted.

The recognition of new species and proving the range of those already known requires a thorough literature search and reference to catalogues such as that of Ellis and Messina (1940 – date). This information, together with the results of evaluation of the samples, should be systematically entered up on formal data sheets.

Fine details of the test surface and ultrastructures are best observed and photographed by SEM. Smooth, lamellar forms give better results by light photomicrography and can be drawn by camera lucida. Internal structures can be revealed by moulds or observed and photographed by the 'non-destructive' method of X-ray microradiography.

ANNOTATED LITERATURE ON TECHNICAL METHODS

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Rouvillois, Armelle and Rosset-Moulinier, Marie (1969). Mise au point d'un petit carottier pour le prélèvement sans perturbation de la partie superficielle des sediments marin. *Cah. océanogr.,* **21**(10):1 – 9

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Schenck, H. G. and White, R. T. (1942). Collecting microfossils. *Am. Midl. Nat.,* **28**:424 – 450

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Vlerk, I. M. Van Der. (1933). The task of the oil paleontologist. *Geologie Mijnb.,* No. 2:15 – 19

Collection and Culture of Live Foraminifera

Adshead, P. C. (1967). Collection and laboratory maintenance of living planktonic foraminifera. *Micropaleontology,* **13**(1):32 – 40

Simple techniques of culture-floating in containers

Arnold, Z. M. (1974). Techniques for the study of living foraminifera: pp. 153 – 206 in *Foraminifera,* vol. 1 (Hedley, R. H. and Adams, C. G., Eds.). Academic Press, London

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Bé, A. W. H., Hemleben, C. and Anderson, O. R. *et al.* (1977). Laboratory and field observations of living planktonic foraminifera. *Micropaleontology,* **23**(2):155 – 179

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Buzas, M. A. (1978). Foraminifera as prey for benthic deposit feeders: results of predator exclusion experiments. *J. mar. Res.,* **36**(4): 617 – 625

Methods of caging Foraminifera

Freudenthal, H. D., Lee, J. J. and Pierce, S. (1963). Growth and physiology of foraminifera in the laboratory, Part 2—a tidal system for laboratory studies on eulittoral foraminifera. *Micropaleontology,* **9**(4): 443 – 448

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Muller, Pamela H.(1974). Sediment production and population biology of the benthic foraminifer *Amphistegina madagascariensis. Limnol. Oceanogr.,* **19**(5):802 – 809

Basic laboratory culture methods

Murray, J. W. (1979). British nearshore foraminiferids: pp. 1 – 68 in *Synopses of the British Fauna (n.s.),* vol. 16 (Kermack, Doris, M. and Barnes R. S. K., Eds.), Academic Press, London

Includes methods of collection of live specimens, staining with Rose Bengal, flotation with heavy liquids, picking, sorting and recognition of wall structure and staining for aragonite

Rouvillois, Armelle (1977). Milioux d'élevage de Foraminifères en aquarium à Paris. *Rev. de Micropaleont.*, **20**(1):53 – 58

UNESCO (1968). *Zooplankton Sampling.* Unesco, Geneva

Disintegration and Concentration

Bolli, H. (1952). Note on the disintegration of indurated rocks. *Micropaleontologist,* **6**(1):46 – 48

Boltovskoy, E. (1966). Methods for sorting of foraminifera from plankton samples. *J. Paleont.*, **40**(5):1244 – 1246
Simple filtration method, most rapid and convenient, followed by classical method of picking out from a petri dish

Carlton, C. M. (1933). A method of concentrating foraminifera. *J. Paleont.* **7**(4):439
Describes bromoform technique in which air-filled Foraminifera are separated from sand by throwing the dried residue on bromoform and sinking the quartz by adding absolute alcohol. Pyritised Foraminifera in shale can be sunk in full-strength bromoform and the shale flakes floated off

Craig, G. Y. and Hogg, J. (1962). A rapid sorting device for microfossils.
Micropaleontology, **8**(1):107 – 108

Gibson, T. G. and Walker, W. M. (1967). Flotation methods for obtaining foraminifera from sediment samples. *J. Paleont.*, **41**(5):1294 – 1297

Hanna, G. D. and Church, C. (1928). Freezing and thawing to disintegrate shales. *J. Paleont.*, **2**:131
See Glaessner (1945, p.37; see 1963 reprint, detailed in main reference list under Glaessner, 1963a) for similar technique using sodium sulphate

Howe, H. V. (1941). Use of soap in the preparation of samples for micropaleontological study. *J. Paleont.* **15**(6):691
Method found useful for sands. Samples washed on 200-mesh screen in warm sudsy water and suspension decanted through another 200-mesh sieve

Kennard, M. C. and Smith, A. J. (1961). A simple micro-sample splitter. *J. Paleont.*, **25**(2):396 – 397
Ingenious device made entirely from glass slides

Laboratory, N. V. De Bataafsche Petroleum Maatschappi (1935).
Recovery of foraminifera by means of flotation. *J. Paleont.*,**9**(8):745 – 746
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Parker, Frances L. (1948). Foraminifera of the Continental Shelf from Gulf of Maine to Maryland. *Bull. Mus. comp. Zool. Harv.*, **100**(2):213 – 241
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Redmond, C. D. (1953). Further notes on the disintegration of shale samples. *Micropaleontologist,* **7**(2):47 – 48

Stevens, C. H., Jones, D. H. and Todd, R. G. (1960). Ultrasonic vibration as a cleaning agent for fossils. *J. Paleont.*, **34**:727 – 730

Stinemeyer, E. H. (1965). Microfossil vacuum-needle segregating pick: pp.276 – 283 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Thiel, T., Thistle, D. and Wilson, G. D. (1975). Ultrasonic treatment of sediment samples for more efficient sorting of meiofauna. *Limnol. Oceanogr.*, **20**(3):472 – 473

Todd, Ruth, Low, Doris and Mello, J. F. (1965). General procedures and techniques applicable to major fossil groups—Smaller Foraminifera: pp.14 – 20 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco
Dangers of contamination and difficulties of sampling. Use of hydrogen peroxide technique, cinnamon oil in gum tragacanth, water soluble vegetable stains, removal of plant debris by carbon tetrachloride

Triebel, E. (1938). Ueber das Auslesen von Mikrofossilien. *Senckenbergiana,* **20**(314):292 – 296
Improved 'Franke's picking tray' with holes at all grid intersections—less movement of tray but tendency of Smaller Foraminifera to stick on edge of holes

Sectioning

Akpati, B. N. (1969). A new technique for serial sectioning of foraminifera. *J. Paleont.*, **43**(4):1046 – 1048

Arnold, Z. M. (1965). An improved instrument for sectioning microfossils: pp. 232 – 238 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Cole, W. S. (1952). Eocene and Oligocene larger Foraminifera from the Panama Canal Zone and vicinity. *Prof. Pap. U.S. geol. Surv.*, **244**:1 – 41
Illustrates half-vertical sections made after the specimen is cut to the equatorial layer and photographed—to give paired thin sections from the same specimen

Croft, W. N. (1950). A parallel grinding instrument for the investigation of fossils by serial sections. *J. Paleont.*, **24**(6):693 – 698

Cummings, R. H. (1950). Oriented thin-sectioning of microfossils. *Contr. Cushman Fdn. foramin. Res.*, **1**(3 – 4):66 – 67

Cummings, R. H. (1952). Developments in micropaleontological technique. *J. Paleont.*, **26**(1):123
Further development of Wood's method of tracing off camera bellows. Bromide paper used on microprojector screen to produce 'trace' photographs for routine measurements. Use of plastic resins for mounting specimens for serial sections—series of cellulose peels taken after etching with dilute hydrochloric acid, care and practice required, difficulties arise through excessive or

insufficient etching or incorrect viscosity of the cellulose

Emiliani, C. (1951). Notes on the thin sectioning of smaller foraminifera. *J. Paleont.,* **25**(4):531 – 532

Hagn, H. (1953). A new method of preparing oriented thin sections of foraminifera and other small paleontologic specimens. *Micropaleontologist,* **7**(1):34

Hansen, H. J. and Lykke-Anderson, Anne-Lise (1976). Wall structure and classification of fossil and Recent elphidiid and nonionid Foraminifera. *Fossils and Strata,* **10**:1 – 37

Hofker, J. (1951). The Foraminifera of the Siboga Expedition. Part III—Ordo Dentata, Subordines Protoforaminata, Biforaminata, Deuteroforaminata. *Uitk. Zool. Bot. Oceanogr. Geol. Geb.,* monogr. IVc, 1 – 513

Castor oil *(Rhicinus)* as clarifier (does not evaporate). Describes sectioning small Foraminifera with Solenhofen chalk and castor oil

Honjo, S. (1960). A study of some primitive *Neoschwagerina* by a new serial section technique. *J. Fac. Sci. Hokkaido Univ.,* ser. 4, *Geol. and Min.* **10**(3):457 – 470

Ground surface etched with an inorganic salt solution (this gives more control than an acid solution) and peels taken with Bioden plastic. They show more detail than is generally visible on thin sections and can be taken every 10 μm.

Kennedy, Clarice M. A. (1978). An improved technique for revealing the internal structure of microfossils by scanning electron microscopy. *J. Paleontol.,* **52**(2):506 – 508

Specimens embedded in polyvinyl acetate which can be dissolved by soaking in acetone (30 – 60 min) after the section is cut. Section then washed in water and dried before mounting for scanning

Kennedy, C. and Zeidler, W. (1976). The preparation of oriented thin sections in micropaleontology: an improved method for revealing the internal morphology of foraminifera and other microfossils. *Micropaleontology,* **22**(1):104 – 107

Kremp, G. (1953). Preparation of oriented sections of microfossils. *Micropaleontologist,* **7**(1):29

Morkhoven, F. P. C. M. Van. (1958). A simplified method of grinding foraminifera. *Micropaleontology,* **4**(2):209 – 210

Pohl, E. R. and Browne, R. G. (1973). A thin section method for ultrasmall paleontologic specimens. *J. Paleont.,* **47**(2):221 – 225

Wood, A. (1948). Sectioning small foraminifera. *J. Paleont.,* **22**(4):530

Microscopy (including Methods of Preparation, including Sectioning for TEM and SEM)

Bellemo, S. (1974). Ultrastructures in Recent radial and granular calcareous foraminifera. *Bull. geol. Instn Univ. Uppsala, N.S.,* **4**:117 – 122

Preparation of sections for SEM examination of wall structures. Etching with sodium hypochlorite to remove organic matrix and glutaraldehyde which fixes protein and dissolves calcite

Deutsch Conger, Susan and Green, H. W. (1976). Preparation of thin-foil specimens for transmission electron microscopy of microorganism tests. *J. Paleontol.,* **50**(5):795 – 798

Grønlund, H. and Hansen, H. J. (1976). Scanning electron microscopy of some Recent and fossil nodosariid foraminifera. *Bull. geol. Soc. Denmark,* **25**:121 – 134

Hansen, H. J. (1968). X-ray diffractometer investigations of a radiate and a granulate foraminifera. *Meddr. dansk geol. Foren.,* **18**(3 – 4):346 – 348

Hansen, H. J. (1970). Electron-microscopical studies on the ultrastructures of some perforate calcitic radiate and granulate foraminifera. *K. danske Vidensk. Selsk. Skr.,* **17**(2):1 – 16

TEM techniques: To obtain replicas of inner surfaces the specimen was embedded with the chambers air-filled and aperture sealed with gum tragacanth. After hardening of Araldite, the specimen was ground to midpoint with frosted glass. Before etching with ethylenediamine tetra-acetate it was replicated 2 – 3 times to remove dust and inner organic membrane and after etching to remove the free etched membrane. Replication with collodion was found to be the most convenient. Describes technique whereby several replicas can be made without losing the specimen

Hansen, H. J. and Reiss, Z. (1972). Scanning electron microscopy of wall structures in some benthonic and planktonic Foraminiferida. *Revta est. Micropaleont.,* **4**(2):169 – 179

Hansen, H. J., Reiss, Z. and Schneidermann, N. (1969). Ultramicrostructure of bilamellar walls in Foraminiferida. *Revta esp. Micropaleont.,* **1**(3):293 – 316

TEM: Specimen ground in Araldite with carborundum paper 600 and polished with MgO powder 0.8 μm; cleaned in ultrasonic vibrator for 5 sec, etched EDTA 3 – 4 min, washed in demineralised water. Dried specimen replicated with collodion or platinum – carbon shadowed peels made; transferred to cut-off grids and replicas dissolved

SEM: Dry specimen embedded in Lakeside 70 on stubs and broken with needle to show septa

Hay, W. W. and Sandberg, P. A. (1967). The scanning electron microscope, a major break-through for micropaleontology. *Micropaleontology,* **13**(4): 407 – 418

Hay, W. W., Towe, K. M. and Wright, R. C. (1963). Ultrastructure of some selected foraminiferal tests. *Micropaleontology,* **9**(2):171 – 195

TEM: Specimen washed in acetone then carbon replicas made under vacuum, calcium carbonate tests then dissolved in HCl; replicas washed in distilled water and picked up on Formvar. A coated electron microscope specimen screen is used for viewing

Hyde, P. and Krinsley, D. (1964). An improved technique for electron microscopic examination of foraminifera. *Micropaleontology,* **10**(4):491 – 493

Jahn, Brigette (1953). Elektronenmikroskopische Untersuchungen an Foraminiferenschalen. *Z. wiss. Mikrosk.,* **61**:294 – 297
Pioneer TEM study on Foraminifera

Jones, D. J. (1956). Use and care of the microscope: appendix A, pp. 337 – 341 in *Introduction to Microfossils.* Harper, New York

Kimoto, S. and Honjo, S. (1968). The SEM as a tool in geology and biology: in *Manual of Micropaleontological Techniques.* McLean Paleont. Lab. Alexandria, Va., USA *(J. Fac. Sci., Hokkaido Univ.,* ser. IV, **14**(1):57 – 59)

Kimoto, S. and Russ, J. C. (1969). The characteristics and applications of the scanning electron microscope. *American Scientist,* **57**(1):112 – 133

Krinsley, D. and Bé, A. W. H. (1965). Electron microscopy of internal structures of foraminifera: pp.335 – 344 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.), W. H. Freeman, San Francisco
TEM: Acetate peel replicas obtained after etching with EDTA for 1 – 2 min, shadowed with platinum – palladium alloy. Replica dissolved in acetone before TEM photography

McGee-Russel, S. M. and Orville, R. E. (1974). Aspects of image analysis of high voltage electron micrographs of air-dried whole mounts of pseudopodial networks of the marine protozoan *Allogromia* (Foraminifera); hand methods and electronic methods: pp.155 – 162 in *High Voltage Electron Microscopy; Image Recording and Resolution.* Academic Press, London

Neumann, Madeleine (1974). Aperçu sur l'apport du microscope electronique à balayage à la connaissance des Foraminifères. *Trav. Lab. Micropal. Univ. Paris,* **6**(3):27 – 70

Oatley, C. W. (1966). The scanning electron microscope. *Science Progress,* **54**(216):483 – 495.
The original description

Paterson, D. (1965). Microscopy in the round. *New Scientist,* **28**:737 – 739.
How the SEM works.

Sylvester-Bradley, P. C. (1969). Aluminium coating in scanning electron microscopy. *Micropaleontology,* **15**(3):366

Walker, D. A. (1978). Preparation of geological samples for scanning electron microscopy: pp. 185 – 192 in *Scanning Electron Microscopy,* vol. I. SEM Inc., A.M.F. O'Hare, Illinois

Wood, A. (1963). Wall structure of foraminifera in polarised light. *Micropaleontology,* **9**(4):432

Special Methods of Preparation and Examination

Anderson, O. R. and Bé, A. W. H. (1978). Recent advances in foraminifera fine structure research: pp. 121 – 202 in *Foraminifera,* vol. 3 (Hedley, R. H. and Adams, C. G., Eds.). Academic Press, London and New York
Chemical fixatives, techniques, fixation procedure for electron analysis, use of glutaraldehyde and anaesthetic ($MgCl_2$)

Arnold, Z. M. (1965). The vacuum oven for impregnating microfossils: pp. 262 – 263 in *Handbook of Paleontological techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Aves, C. (1958). Foraminiferal fixatives and preservatives. *Gulf Coast Ass. geol. Socs. Field Trip Guidebook,* pp. 48 – 56

Blow, W. H. (1955). Dissection of highly perforate calcareous foraminifera. *Micropaleontology,* **1**(2):190

Boltovskoy, E. and Wright, R. (1976). Cytological techniques: chap. 11, pp. 309 – 312 in *Recent Foraminifera.* Dr W. Junk, The Hague

Brotzen, F. (1936). Foraminiferen aus dem schwedischen untersten Senon von Erikskal in Schonen Sweden. *Sver. geol. Unders. Afh.,* ser. C, **30**(396):1 – 206
Pp. 24 – 25 give use of methylene blue at 1:150 parts in water to stain a siliceous or argillaceous matrix. Radiolaria and agglutinating Foraminifera go dark blue—also silicified Foraminifera from the chalk

Dunbar, C. O. and Henbest, L. G. (1942). Pennsylvanian Fusulinidae of Illinois. *Bull. Ill. St. geol. Surv.,* **67**:1 – 218
Staining of ground surfaces by methylene blue, malachite green or alizarine red

Gorycki, M. A. (1971). A compound embedding technique for the microscopical study of living and fossil foraminifera. *Micropaleontology,* **17**(3): 492 – 500

Grayson, J. F. (1956). The conversion of calcite to fluorite. *Micropaleontology,* **2**(1):71 – 78

Hansen, H. J. (1968). A technique for removing gold from plated calcareous microfossils. *Micropaleontology,* **14**(4):499 – 500

Henbest, L. G. (1931). The use of selective stains in paleontology. *J. Paleont.* **5**(4):355 – 364
Selective staining techniques for specimens and thin sections, malachite green, alizarine, also calcium carbonate and aragonite tests

Hofker, J. (1927). The Foraminifera of the Siboga Expedition. Part I—Tinoporidae, Rotaliidae, Nummulitidae, Amphisteginidae. *Uitk. Zool. Bot. Oceanogr. Geol. Geb.,* monogr. IVa: 1 – 78

Kornicker, L. S. (1954). Elimination of static charge from celluloid covered micropaleontological slides. *Micropaleontologist,* **8**(1):36

Troelsen, J. C. (1954). Glass needles used in dissection of foraminifera. *Micropaleontologist,* **8**(1):37

Upshaw, C. F., Todd, Ruth and Allen, B. D. (1957). Fluoridization of microfossils. *J. Paleont.,* **31**(4):793 – 795

Walker, D. A., Linton, Anne E. and Schafer, C. T.

(1974). Sudan Black B: a superior stain to Rose Bengal for distinguishing living from nonliving foraminifera. *J. foramin. Res.*, **4**(4):205 – 215

Walton, W. R. (1952). Techniques for recognition of living Foraminifera. *Contr. Cushman Fdn foramin. Res.*, **3**(2):56 – 60

X-ray and Spectrochemical Analysis

Bender, M. L., Lorens, R. B. and Williams, D. F. (1975). Sodium, magnesium and strontium in the tests of planktonic foraminifera. *Micropaleontology*, **21**(4):448 – 459

Blackmon, P. and Todd, R. (1959). Mineralogy of some foraminifera as related to their classification and ecology. *J. Paleont.*, **33**(1):1 – 15

X-ray diffraction of both powdered and individual specimens. The importance of magnesium in classification

Craig, H. (1965). The measurement of oxygen isotope paleotemperatures: pp.3 – 24 in *Stable Isotopes in Oceanographic Studies and Palaeotemperatures* (Tongiorgi, E., Ed.). Univ. Lab. Geol. Nucleare. Cons. Naz. Ricer., Pisa

Dodd, J. R. (1965). Preparing fossils and shells for chemical analysis: pp. 384 – 388 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.), W. H. Freeman, San Francisco

Emiliani, C. (1955). Mineralogical and chemical composition of the tests of certain pelagic foraminifers. *Micropaleontology*, **1**(4):377 – 380

Spectrochemical analysis of optical and radiant energy emmision spectra of Ti, Al, Fe, Mn, Mg and Sr of Quaternary planktonic Foraminifera. Specimens vaporised at high temperatures. X-ray diffraction by powder technique

Emiliani, C. and Epstein, S. (1953). Temperature variations in the lower Pleistocene of Southern California. *J. Geol.*, **61**(2):171 – 181

Mass spectrometric analysis of O^{18}:O^{16} ratios in Foraminifera from the Lomita marl

Emrich, K., Ehhalt, D. H. and Vogel, J. C. (1970). Carbon isotope fractionation during the precipitation of calcium carbonate. *Earth Planet Sci. Lett.*,**8**(5):363 – 371

Calcium carbonate is deposited in equilibrium with the stable isotopes of carbon, O^{12} and O^{13}. The relative abundance of these isotopes will depend on temperature and the isotopic constitution of the sea water, although the temperature effect is small, approx. 0.03 per thousand per °C

Hecht, A. D. (1976). The oxygen isotopic record of foraminifera in deep-sea sediment: pp. 1 – 43 in *Foraminifera*, vol. 2 (Hedley, R. H. and Adams, C. G., Eds.). Academic Press, London

Comprehensive review of methodology and application. Sample of 50 – 100 individuals of the species needed (3 – 5 mg) to produce sufficient CO_2 gas for analysis by mass spectrometer. Crushed between glass plates, ultrasonically cleaned and washed with water or methanol. Reacted *in vacuo* with 100 per cent phosphoric acid at 25°C or 50°C for 12 – 24 h. Gas purified of water vapour over dry ice

Hedley, R. H. (1957). Microradiography applied to the study of foraminifera. *Micropaleontology*, **3**(1):19 – 28

X-ray microscopy by contract microradiography

Hooper, K. (1959). X-ray absorption techniques applied to statistical studies of foraminifera populations. *J. Paleont.*, **33**(4):631 – 640

Nondestructive methods for measuring internal structures applied to *Operculina*—measurements made directly off enlargements (waterproof paper)

Hooper, K. (1964). Electron probe microanalysis of Foraminifera; an exploratory study. *J. Paleont.*, **38**(6):1082 – 1092

Technique allows study of variation of elements in different layers—even different crystals. The foraminifer is embedded in polystyrene and polished sections placed under the probe. Ca, Fe, Si, Mn, Mg, Cu detected in *Operculina* and other modern genera including *Elphidium* and *Quinqueloculina*

Lipps, J. H. and Ribbe, P. H. (1967). Electron-probe microanalysis of planktonic foraminifera. *J. Paleont.*, **41**(2):492 – 496

Shackleton, N. J. (1974). Attainment of isotopic equilibrium between ocean water and the benthonic foraminifera genus *Uvigerina*, isotopic changes in the ocean during the last glacial: pp. 203 – 210 in *Les Methodes Quantitative d'Étude des variations de climat au cours du Pleistocene* (Lalou, C., Ed.). Gif-sur-Yvette, France. (Fr., Cent. Natl. Rech. Sci., Colloq. Int., 219).

Switzer, G. and Boucot, A. J. (1955). The mineral composition of some microfossils. *J. Paleont.*, **29**(3):525 – 533

Technique and equipment for X-ray diffraction study of uncrushed Foraminifera. Allows calcite and aragonite to be differentiated, nature of alteration and agglutinated minerals

Illustration

Albani, A. D. (1964). Photography of microfossils. *Micropaleontology*, **10**(3):396 – 398

Apparatus using Zeiss luminar lenses and bellows with universal stage for orientating specimen for minimum depth of field

Bé, A. W. H., Jongebloed, W. L. and McIntyre, A. D. (1969). X-ray microscopy of Recent planktonic foraminifera. *J. Paleont.*, **43**(6):1384 – 1396

Benson, R. H. (1965). Photography of microfossils: pp. 433 – 446 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Use of Leitz photographic apparatus with Lieberkuhn mirror system and lucite lighting stage assembly. Immersion of specimen in liquid with high R.I. such as glycerol, high viscosity and soluble in water or alcohol. Coating by ammonium chloride or magnesium dioxide from burning ribbon. Use of dyes

Cummings, R. H. (1956). Preparation of microfossils for photography. *Micropaleontology,* **2**(4):402

Douglass, R. C. (1965). Photomicrography of thin sections: pp. 446 – 456 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Evitt, W. R. (1949). Stereophotography as a tool of the paleontologist. *J. Paleont.,* **23**(5): 566 – 570

Fournier, G. (1954). Use of the pinhole diaphragm in photomicrography. *Micropaleontologist,* **8**(3): 58 – 62

Fournier, G. (1956). New methods and techniques in the photography of microfossils. *Micropaleontology,* **2**(1):37 – 56

Hanna, G. D. (1931). Illustrating fossils. *J. Paleont.,* **5**(1):49 – 68
An excellent early paper on the principles involved. Covers preparation of plates for printing, half-tones, zinc etching from stipple board, photogravure, photography and drawing. Use of camera lucida and measuring specimens

Isham, L. B. (1965). Preparation of drawings for paleontologic publication: pp. 459 – 468 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Kier, P. M., Grant, R. E. and Yochelson, E. L. (1965). Whitening fossils: pp. 453 – 456 in *Handbook of Paleontological Techniques* (Kummel, B. and Raup, D., Eds.). W. H. Freeman, San Francisco

Kornicker, L. S. (1953). A method of mounting microfossils for photography. *Micropaleontologist,* **7**(4):32

Mangin, J. P. (1953). Photography of thin sections. *Micropaleontologist,* **7**(3):67

McLean, J. D. (1959). Photomicrography of opaque specimens: Rept. 3, pp. 5 – 11 in *Manual of Micropaleontological Techniques.* McLean Paleont. Lab. Rep. Alexandria, Va., USA

Palmer, Allison (1965). Preparation of plates for paleontologic publication: pp. 456 – 459 in *Handbook of Paleontological Techniques.* (Kummel, B. and Raup, D. Eds.). W. H. Freeman, San Francisco

Pessagno, E. A. (1960). Thin-sectioning and photographing smaller foraminifera. *Micropaleontology,* **6**(4):419 – 423

Reeside, J. B. (1930). The preparation of paleontologic illustrations. *J. Paleont.,* **4**(3):299 – 308
Notes on photography, layout of drawings, etc.

Wallis, T. E. (1955). Drawing from the microscope. *J. R. microsc. Soc.,* **75**(2):77 – 87
Freehand drawing, camera lucida, assembling and lettering

Wood, A. (1945). A rapid method of making accurate drawings of small microscopic objects. *Proc. Geol. Ass.,* **56**(1):18 – 19
Use of camera bellows and tracing paper

Organisation

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Chapter 3

The Living Foraminifer

Unique animals.

(Hedley, 1964)

The micropalaeontologist is concerned with the abandoned, dead shells of Foraminifera and classification of fossil species proceeds entirely upon the basis of the morphology of the hard parts or test. However, he requires a knowledge of the live animal because the morphology and the evolutionary changes so important in stratigraphy can only be understood when the adaptive function of the test in the living animal is known. Also, as will be seen, study of the soft parts and of life history has revealed a number of remarkable features and helped to solve some long-standing problems in the palaeontology of the group.

Foraminifera are single-celled animals (phylum Protozoa) and belong to the same class (Rhizopoda or 'root feet') as *Amoeba*, distinguished by temporary extrusions of the protoplasm or pseudopodia. Foraminifera differ from *Amoeba* in that the pseudopods are fine and hair-like and anastomose together to form a spreading, reticulate network, as well as in the possession of either a gelatinous or a hard, agglutinated or calcareous test.

It must not be thought that because Foraminifera are single celled they are necessarily simple animals. The single cell of the protozoan has to carry out many functions that may be carried out by a range of specialised cells and tissues in the Metazoa including, in Foraminifera, the construction of an architecturally complicated test. This is reflected in the complexity of the protozoan cell with its numerous organelles, as revealed by the electron microscope (figure 3.1).

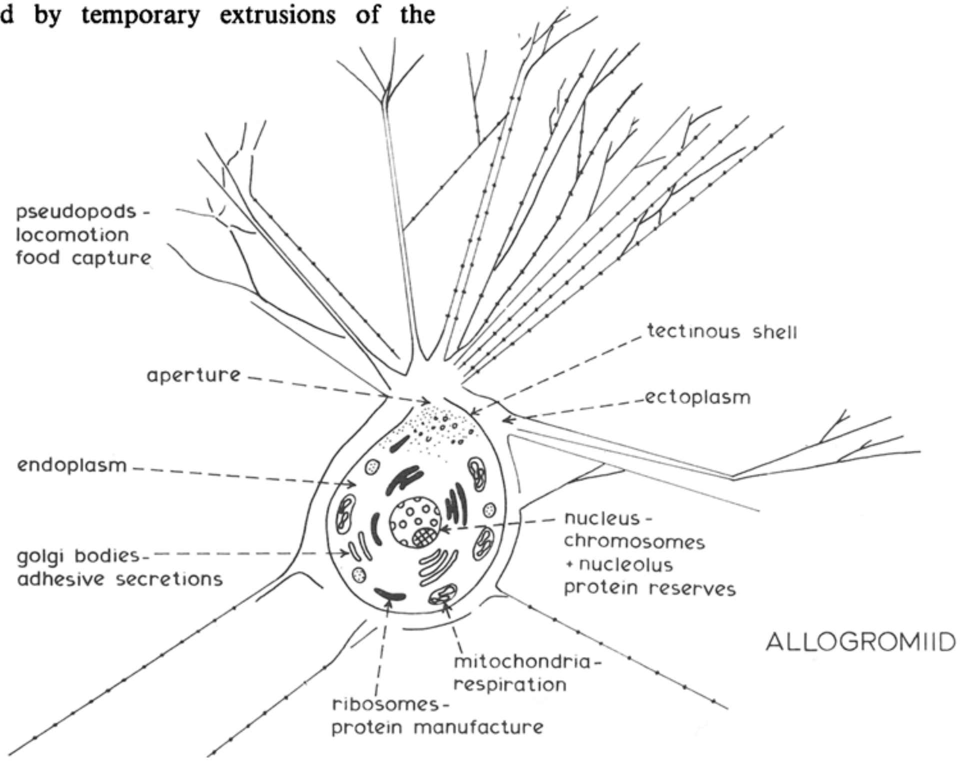

Figure 3.1 Basic soft part morphology, allogromiid

THE STRUCTURES OF THE CELL

The most primitive order, the Allogromiida, includes naked genera such as *Allogromia, Myxotheca* and *Shepheardella.* Here, the test is an organic, gelatinous sac-like structure, 1 – 10 μm thick, composed of glycoprotein (proteinaceous mucopolysaccharide, according to Hedley, 1964) and referred to as tectin. It is an internal structure (figure 3.1) surrounded by ectoplasm (a clear gel-like cytoplasm) immediately external to the primary cell membrane (pellicle or plasmalemma) which contains the dense sol-like endoplasm. In advanced Foraminifera such as the globigerinids (figure 3.2), the organic layer becomes an inner lining to the calcareous test. It should be noted that the cytoplasm everywhere has the capacity for membrane formation and recombination.

Most structures occur in the endoplasm. The overall organisation of the cell is controlled by the nucleus. This is confirmed by the consequences of its removal which leads to disorganisation, failure to digest and eventual death. It has a porous envelope for communication with the rest of the cell and contains the chromosomes which bear the genetic codes needed to produce new cells and are the only structures capable of identical reduplication. There are 7 in *Myxotheca arenilega,* 18 in *Rotaliella heterocaryotica* (9 in *R. roscoffensis* but twice as large) and 24 in *Patellina corrugata* (Grell, 1973). These numbers are constant, which indicates that the chromosomes are regularly distributed to daughter cells on reproduction. The nucleolus is probably responsible for protein reserves.

There is always one nucleus but there are multinucleate development phases. The nuclei may be all alike (homokaryotic) as in *Spirillina* or there may be two kinds (heterokaryotic) — generative nuclei which take part in reproduction and somatic nuclei which take part in some processes and then die, as in *Rotaliella* (Grell, 1973).

The products of metabolic processes are transported through the cell via a continuous network of membranous canals—the endoplasmic reticulum. Granules may coat the outside; these are the ribosomes which synthesise proteins. Also, the ribosomes commonly occur free in the ground cytoplasm. Membranous sacs free of granules also occur; these are the Golgi complexes which function in the production of polysaccharides as

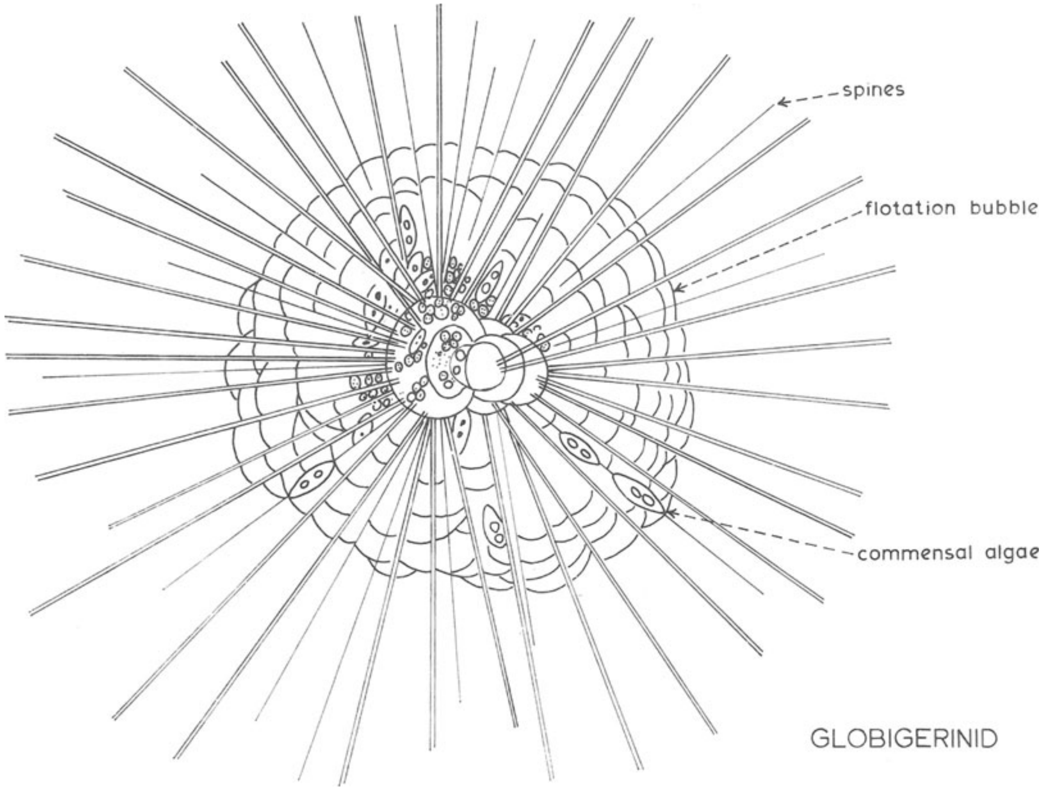

Figure 3.2 Basic soft part morphology, globigerinid

well as mucoid substances and may also be concerned with the packaging of enzymes into the lysosomes. The lysosomes are small vesicles that surround the food vacuoles and deliver their contents during digestion (see further discussion below).

The 'power stations' of the cell are the mitochondria. These are sausage shaped with two membranes, the inner forming invaginations in the outer. The large surface area reflects the function of this organelle, which is to store the energy of oxidation by synthesis of adenosine triphosphate (ATP) until required for energy-consuming reactions.

The most striking structures of the ectoplasm are the pseudopods. These are granular threads that stream out in all directions, reaching lengths of up to three times the diameter of the test (figure 3.1). They may follow a 'guide rhizopodium' and form a distinct trunk-like mass issuing from the aperture (podostyle) with linear elements that fuse and divide to form a broadly ramifying network. Frankel (1975) has shown that a distinct podostyle is formed by the multichambered, agglutinated species *Miliammina fusca* when it is living within the sediment. Under these confined conditions the pseudopods are concentrated into bundles rather than spread out, perhaps in order to push aside and probe through the sedimentary grains. In those species which live within the sediments (infaunal) or live on it (epilithic), the net of pseudopodia developed below the surface becomes an important binding agent (Nyholm, 1957), strong enough to bind reefal sands into an aggregate that can withstand wave action, as has been observed by Ross (1972c) on the Great Barrier Reef.

The tectin wall may be thickened near the aperture in Allogromiids and this oral structure (stomostyle) is turned out (everted) when the pseudopods which can be traced into the endoplasm are extruded (Hedley, 1964).

An oscillatory two-way movement is detectable in the pseudopods. This has been explained as due to two semi-cylindrical units moving in opposite directions as a result of shearing forces (Jahn and Rinaldi, 1959) or by a relatively solid axis moving inwards while a more fluid outer layer moves outwards (Kavanau, 1962). The granules may be mitochondria, and opaque particles which have been observed may be waste particles concentrated as 'stercomata'. The pseudopods can expand and contract and are thrown out on one side—'shot out' in the graphic phrase of Jepps (1942)—and retracted on the other side in locomotion. Proceeding in this way, hauling itself along by its pseudopodia, speeds of a few millimetres an hour may be achieved.

Sheehan and Banner (1972) and Banner and Williams (1973) have shown that very similar pseudopodial networks are a feature of calcareous genera such as *Elphidium* and *Ammonia*. Here the pseudopods arise from ectoplasm which appears to be largely concentrated in the apertural and umbilical regions and covers the last chamber. Speeds of movement of up to 2 mm/h were noted for *Ammonia*.

In Globigerinids a fine net of pseudopods, 'resembling a cobweb of very fine dimensions' (Anderson and Bé, 1976) is supported by the spines which rise from the calcareous test and radiate out in all directions. The Globigerinids are free-floating members of the plankton in the surface waters of the open ocean. Here, the ectoplasm which is frothy and highly vacuolated surrounds the test completely. A vesicular 'fibrillar system' developed in the vacuoles may aid in flotation and control vertical diurnal movements in the water column (Zucker, 1973). In *Hastigerina*, a definite flotation bubble is developed up to 2 mm in diameter (figure 3.2). However, even these pelagic forms can creep along various substrates and oar themselves along just below the surface film of sea water by means of their pseudopods.

The strength and adhesiveness of the pseudopods and their effectiveness in food gathering and test construction is indicated by the ability of *Ammonia* to drag quartz grains along, equal to the test diameter, for several millimetres.

NUTRITION

The food of Foraminifera includes unicellular algae, especially diatoms, other protozoans and small metazoans including crustaceans such as copepods. In addition, according to Muller and Lee (1969), a proportion of bacteria is also an indispensable element in their diet. The pseudopods which are able to become sticky, possibly as a result of secretions produced by the Golgi apparatus (Anderson and Bé, 1976), may also be able to attract algae such as dinoflagellates (Christiansen, 1971) and even paralyse small animals.

Solid food may be carried through the aperture and digested with the help of enzymes secreted by the lysosomes or partly digested in place (phagocytosis). Liquids and macromolecules are taken up by invagination of the cell wall and pinching off of the vesicles so formed—usually at the tips of the pseudopods (pinnocytosis), as described by Sheehan and Banner (1972).

The capture of a crustacean and its digestion have been graphically described by Bé *et al.* (1977):

> When a crustacean comes into contact with *Hastigerina pelagica's* spines, the prey is immediately and inextricably snared by the rhizopodia. The great mechanical stress to which the foraminifer is subjected and the extraordinary ability of the rhizopodia to adhere to several actively pulling crustaceans at the same time are worthy of closer observation. Despite strong efforts to escape, the prey is gradually drawn into the bubble capsule, displacing some bubbles in the process. An adhesive substance is released from vacuoles within the rhizopodia which cover the surface of the prey. The rhizopodia penetrate into crevices in the cuticle of the prey, invade the underlying soft tissue and engulf liquid droplets and small particles of tissue that are released by the dying cells. Engulfed particles of food are carried by rhizopodial streaming into the foraminiferal cytoplasm, where food vacuoles containing the engulfed prey tissue become converted into digestive vacuoles.

In many species of Foraminifera, particularly in Globigerinids and Larger Foraminifera, various algae occur in the endoplasm as well as in the ectoplasm in an association which strongly suggests a symbiotic relationship (living together for mutual benefit). Both green algae (Zoochlorellae—mostly *Chlorella*) and golden/brown algae (Zooxanthellae—mostly dinoflagellates) occur. The symbionts may be attracted to their hosts, as Ross (1972c) noticed that several actively swimming dinoflagellates commonly congregated near *Marginopora.* Their density throughout the protoplasm in this species imparted a distinct yellow-brownish green colour to the foraminifer and was found to be strongly controlled by light. Specimens which had lain on one side for some time became much darker on the upper side with up to 16 symbionts per chamber compared with 2 – 4 on the poorly lighted side. The symbionts are evidently strongly phototropic. In *Sorites* and *Archaias* they are concentrated beneath the test wall and move actively through the host cytoplasm and through the stolons between the chamberlets (Leutenegger, 1977).

Work on the ultrastructure of *Globigerinoides sacculifer* by Anderson and Bé (1976) reveals at least three species of symbionts. During the day these occur mainly in the outer net of fine pseudopodia. In the evening they become surrounded by pseudopods and sequestered in the vacuoles of the ectoplasm and are finally carried through the aperture into the endoplasm. During the night it appears that dense deposits, occasionally seen in the membranous folds of the symbionts when they are in the ectoplasm, may be transferred to the host cytoplasm. In the morning the symbionts are carried out again and transferred along the spines to the net of pseudopods, where they can carry out photosynthesis under the most favourable conditions. No evidence of digestion of the algae was found, so the symbionts were not being used directly as food particles.

As well as symbiosis with algae, the phenomenon of 'chloroplast symbiosis' has also been discovered in the calcareous, brackish water and marsh species, *Elphidium williamsoni* and *Haynesina germanica* (= *Nonion germanicum*), Christensen (1977). In these small, benthonic species, chloroplasts obtained by ingestion of algae, probably diatoms, continue to function as transplants in the endoplasm of the foraminifers. As the chloroplasts are small, 2 – 3 μm in diameter, they can easily be passed through the small, multiple apertures and foramina of these species. Up to 100 000 occur sequestered in the endoplasm of one individual of *E. williamsoni*, and the products of their photosynthetic activity provide a considerable energy source.

It is difficult to tell at this stage of research to what extent the algae or sequestered chloroplasts are necessary to different foraminifer species. However, vigour and $CaCO_3$ productivity have been related to the presence of symbionts (Röttger, 1972; Muller, 1978), and it is tempting to ascribe the restricted range of *E. williamsoni* to its symbiotic habit and relation to particular littoral diatoms. The algae supply oxygen which may be of benefit when the foraminifer draws calcium from sea water to build its test (as in the analogous case of the Corals in association with Zooxanthellae). Such a partnership probably accounts for the rate of carbonate shell production in calcareous Larger Foraminifera, which is 20 – 100 times as great as in smaller benthonics (Ross, 1974). They may also bind carbonic acid and take up nitrate and phosphates. Röttger (1973) has described the remarkable case of *Heterostegina depressa* which can grow without ingesting food other than that provided by its symbionts. It is apparently able to lead a sessile mode of life inside a hyaline sheath secreted by the ectoplasm. The sheath is fixed to the substrate by branched processes and the foraminifer can move about inside by means of its pseudopodia.

According to Hedley (1964) the various colours of protoplasm that have been reported are largely a reflection of the contained symbiotic algae and accumulated wastes as well as cytoplasm pigments and may therefore be changeable. The colours include: vivid sky blue, *Alveolinella;* pale grey-green, *Operculina*; green, *Heterostegina, Elphidium (crispum), Amphistegina* (also with red flecks); lavender, *Peneroplis;* red to dark brown, *Discorbis* (Myers, 1942). Ross (1972c) notes that *Marginopora* can be distinguished from *Amphisorus* by its yellowish – brownish green protoplasm. Distinctions can also be made at the species level in *Elphidium.* In the Dovey estuary (Wales), *Elphidium williamsoni* is generally green, while *E. waddensis* is golden-brown when recovered from the same samples. However, *Allogromia laticollaris* is orange when grown in cultures containing abundant algae, but white or grey when cultured on bacteria or corn starch (Arnold, 1955).

In summary it appears that, as well as exploiting the possibilities of symbiosis in both the benthonic and planktonic realms, Foraminifera also exploit all the six major classes of food resource available to benthonic invertebrates according to Walker and Bambach (1974). These are: dissolved and colloidal organic molecules; organic rich grains (fungal and algal coated and including faecal pellets); particulate organic detritus; live plants; live animals; dead organisms. This success is due to the versatility of the pseudopodial network and explains the abundance of the subclass across the broad spectrum of marine environments. It also helps to explain the great variety of test shapes, coiling modes and apertural modifications in the group, discussed in chapter 4.

REPRODUCTION

During the nineteenth century it gradually became clear that many species of Foraminifera constantly occur in two distinct size groups (dimorphism). It is particularly well marked in Larger Foraminifera such as *Nummulites,* in which it was first pointed out by De La Harpe (1879a) (plate 1). The biological explanation of dimorphism was discovered by Lister (1895), when working on *Elphidium crispum,* to be the result of the alternation of two generations with different kinds of reproduction. Further studies (Jepps, 1942, 1956; Lister, 1903) have shown that this involves an asexual generation (agamont) with a small proloculus (microsphere) and a sexual generation (gamont) with a large proloculus (megalosphere). As this cycle has been found to occur generally in all the main groups of Foraminifera it is appropriate to look at it in detail in the closely studied species, *Elphidium crispum.*

In asexual reproduction, reduction division of the nucleus takes place (meiosis) to give daughter cells with half the number of chromosomes (haploid). These haploid 'agametes' grow to give the haploid, sexually reproducing, gamont generation (A form). When the gamont has reached a certain size sexual reproduction takes place without further reduction of the chromosomes to give haploid gametes (mitosis). These are flagellate and free swimming. They leave the test, meet and fuse to produce a resting stage (zygote) which gives rise to the new, diploid, asexually reproducing, agamont generation (B form). This process with one generation diploid and one haploid is 'heterophasic alternation of generations' and is general in the Protozoa. However, the possession of a diploid, asexual generation in all foraminiferal species studied (Hedley, 1964), as in plants, is unique among Protozoans and, indeed, among animals.

The haploid gamont has a single nucleus only, but in the B form nuclear multiplication takes place before the zygote hatches, so it is multinucleate throughout life. The B form is also larger and develops more chambers than the A form.

The complete cycle for *E. crispum* takes two years in the shallower parts of the English Channel, although it may be delayed at deeper stations. Asexual reproduction reaches a peak in April. All the protoplasm leaves the test and within the protection of a 'halo' of pseudopods separates into the daughter cells which secrete a calcareous megalosphere before dispersal. Chambers are added at the rate of about two per day. Most are full grown by the end of the summer and pass the winter in a state of inactivity. Sexual reproduction begins early in the second spring as temperatures begin to rise. The biflagellate gametes are produced inside the test and escape via the aperture and septal pores, leaving it undamaged. The gametes conjugate outside in the open sea to produce zygotes and the B form then develops and matures during the second summer. They always appear to be less abundant than the A forms and Jepps found that megalospheric forms outnumber microspheric forms by about 30 to 1 throughout the winter months.

That the same cycle occurs in other major groups of forams, including primitive allogromiids, is shown by figure 3.3 which illustrates the reproduction phases in *Myxotheca arenilega*. Again, thousands of flagellate gametes, each with a full complement of organelles, are produced at mitosis (Angell, 1971) to give a diploid zygote and, although unilocular, the B form can be seen to be distinctly larger.

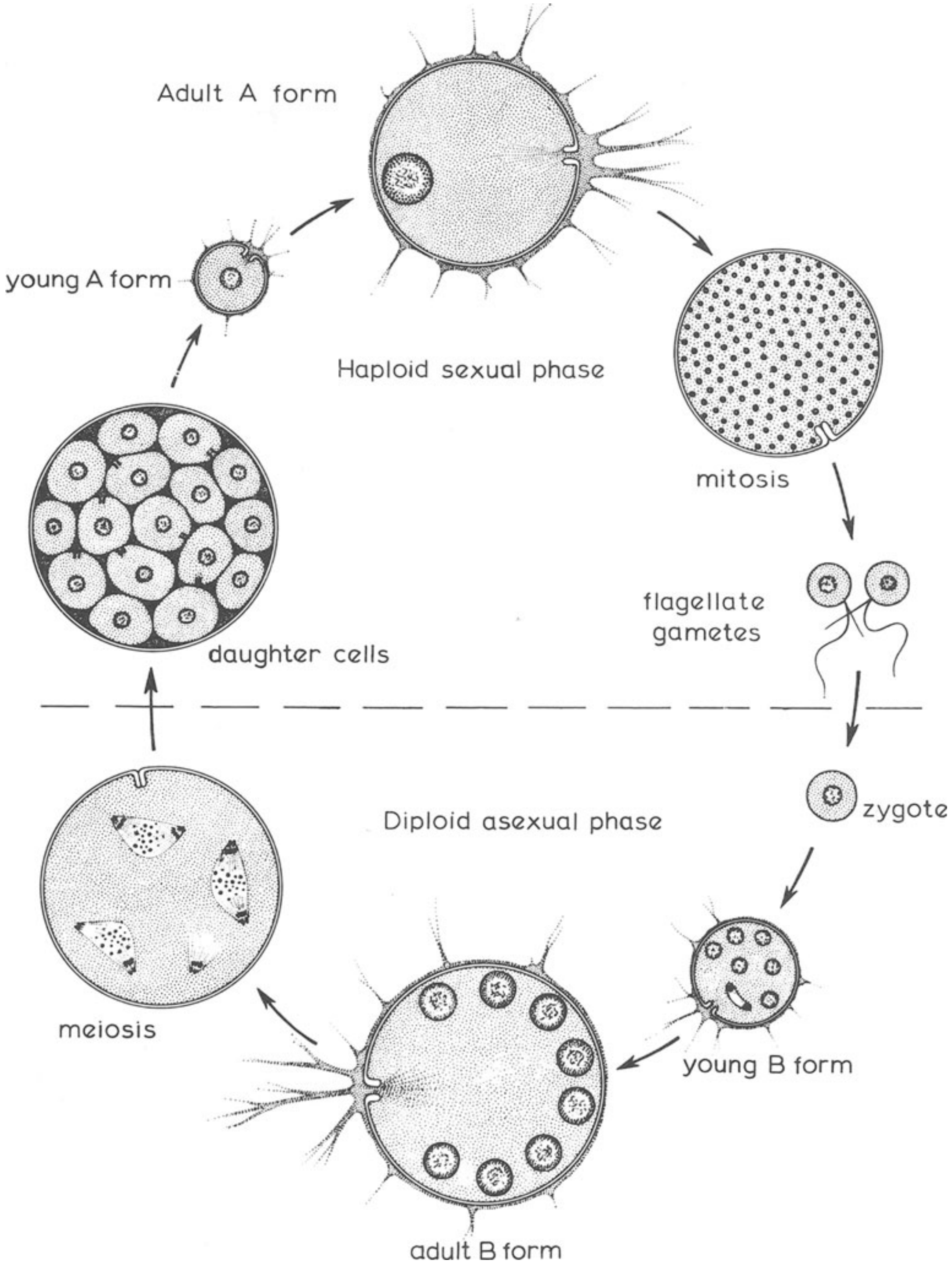

Figure 3.3 Alternation of generations in *Myxotheca arenilega*. After Grell (1973)

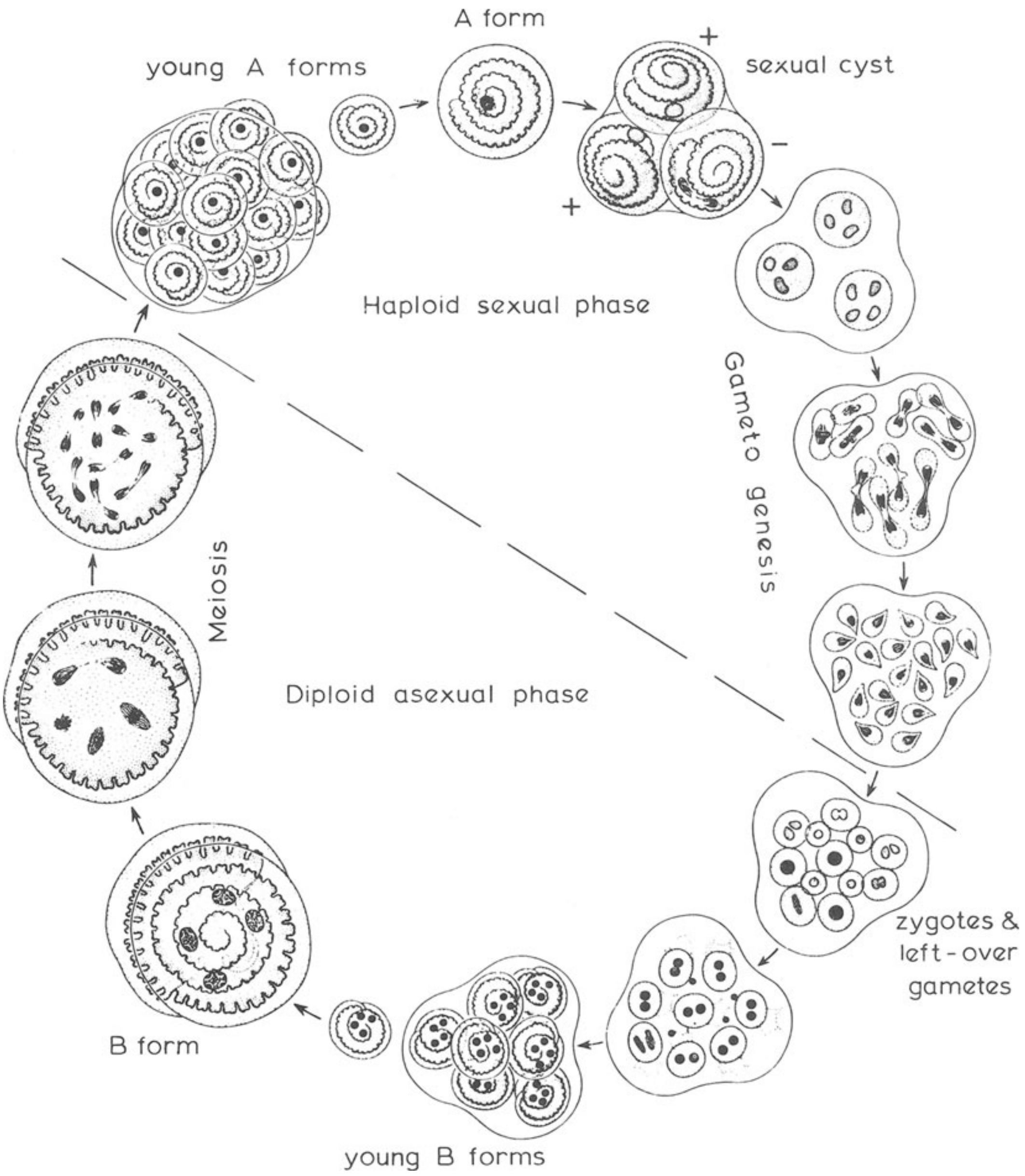

Figure 3.4 Alternation of generations in *Patellina corrugata*. After Grell (1973)

Interesting variations on the general theme are shown by other allogromiids and the Spirillinidae (including the possibly related *Rotaliella*). In these groups the gametes are amoeboid rather than flagellate, although otherwise the ultrastructure appears to be the same (Schwab, 1976). The life cycle of the multichambered, calcareous spirillinid, *Patellina corrugata* was first worked out by Myers (1935), supplemented by Grell (1959). The phases are shown in figure 3.4. The adult B form builds a protective cyst for asexual reproduction and the daughter cells secrete the initial, undivided spiral part of their tests (juvenarium) using the parent as a source of calcium before breaking free. At maturity the A forms congregate in groups of up to nine individuals inside sexual reproduction cysts. According to Grell the A form is sexually differentiated and the gametes only fuse with those from a parent of the opposite 'sex'. As shown in figure 3.4 both sexes are normally present in the aggregates. In a case where two plus individuals (with 3 nuclei) are associated with one minus individual (with 4 nuclei) only 8 zygotes will be produced, the spare nuclei being consumed as food. Although this species has an undivided juvenarium, and no true proloculus is distinguishable, pronounced dimorphism is exhibited and the B form is clearly larger.

The low numbers of gametes produced in *P. corrugata* is doubtless connected with the development of the protective cyst around the multiple aggregates of the adult sexual generation. In those genera like *Elphidium* where the gametes are flagellate and released into the open sea, vast numbers are produced—described by Jepps (1956) as, 'a dancing multitude of biflagellate swarm spores. They usually leave the shell in the middle of the night, in a milky stream as if the parent were smoking hot'. An attempt to estimate the actual numbers involved has been made by Bé and Anderson (1976) in their study of gametogenesis in the planktonic globigerinid, *Globigerinoides sacculifer*. Counts made from thin sections of fixed and stained specimens indicate that the number produced may exceed three million, each about 5 μm in diameter. As Bé and Anderson point out, although planktonic Foraminifera are abundant in the water column, they are so widely spaced that only the production of myriads of gametes can ensure cross-fertilisation. Even so, it appears that A forms always greatly outnumber the B forms.

Special methods are employed to aid the disposal of gametes in the multilocular, calcareous discorbid, *Tretomphalus bulloides* (figure 3.5) with pairing (plastogamy) to ensure cross-fertilisation. The B form is attached and asexual reproduction takes place beneath a protective cover of agglutinated debris (cyst). Some 200 embryos are produced which dissolve the test wall to escape. The A form also lives as an attached form until it has developed up to 18 chambers, when it again forms a cyst. This is followed by the formation of a large, spherical float chamber filled with gas. The foraminifer then bursts out of the cyst and floats to the surface. Sexual reproduction with formation of flagellate gametes takes place after pairing with another individual that has reached the planktonic stage. The float chambers are brought together by movements of the pseudopodia and the gametes are discharged through special pores. This process is probably made easier if the coiling directions are the same. The fused gametes, which are the product of two different parents, then sink to the bottom and form a zygote which gives rise to the attached benthonic, microspheric phase.

In *Marginopora* a number of cyclic 'reproduction chambers', without partitions, are produced at maturity by the asexual form. Up to 150 embryos are nurtured in these special chambers and are released by breakdown of the peripheral margin. The rest of the reproduction chambers also rapidly disintegrate under reefal conditions, so that quite soon only a jagged remnant of the first reproduction chamber is observable (Ross, 1972c). The life cycle in this large, tropical genus also appears to be longer than that of genera such as *Elphidium* and *Ammonia* in the temperate zone, and asexual reproduction may not occur until growth has proceeded for two years or more. The largest individuals, up to 3 cm diameter, showed no reproduction chambers and may have lived, still growing, below the depth limit for reproduction. Jepps (1942) showed that *Elphidium crispum* took longer to mature at greater depths, and tank experiments (Bradshaw, 1955; Murray, 1963) confirm that reproduction occurs earlier under optimum conditions whereas at low temperatures and with decreased food growth may continue longer, resulting in larger individuals.

The alternation of generations is not strict in all species and asexual reproduction may be repeated giving an intermediate A form (trimorphism of Hofker, 1925) or even a series of A forms with different sized megalospheres (polymorphism). Under tank conditions, only asexual reproduction has been observed in some species (Lecalvez, 1950; Ross, 1972c). McEnery and Lee (1976) report the interesting case of *Allogromia laticollaris*, in which three different strains all show different styles of this apogamic reproduction, differing from the 'classical' mode.

GENERAL HABIT

The majority of Foraminifera live on the sea bed (benthonic), while a small number of genera and species, often represented by a very large number of individuals, float freely in the water column of the open ocean. A relatively small number of benthonic genera live permanently attached with their tests firmly cemented to various objects on the sea floor. Different species are adapted to the full range of temperatures and salinities that occur in the oceans as well as marginal marine environments, and some groups can withstand low levels of oxygen and alkalinity and flourish below the depth of calcium carbonate dissolution (CCD) on the abyssal plain.

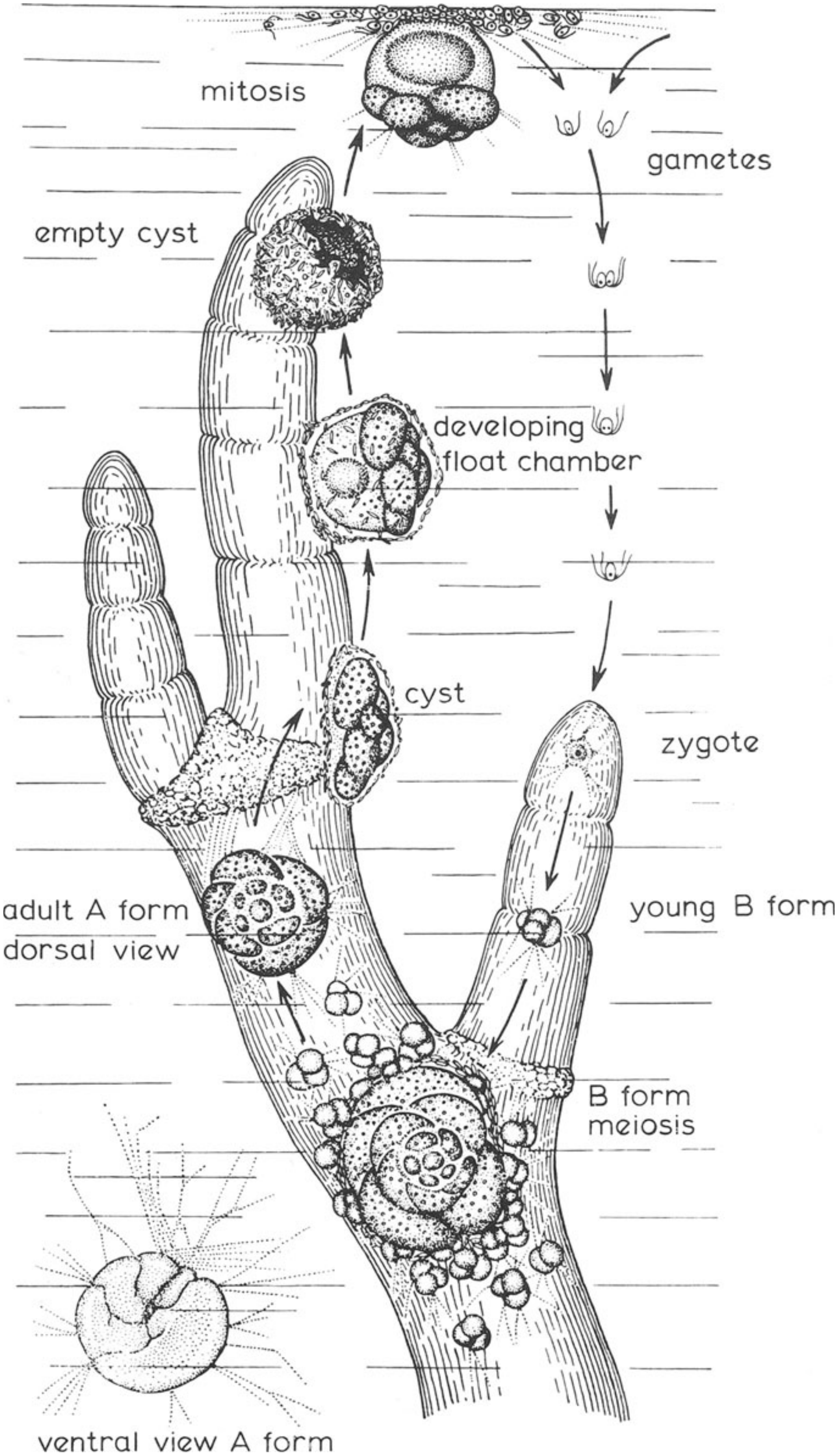

Figure 3.5 Alternation of generations in *Tretomphalus bulloides*. After Grell (1973)

The free benthonic forms occur on most sediments (epilithic) and also live within them infaunally to depths controlled largely by the onset of anaerobic conditions. Ross (1972c) has described how even large discoid species such as *Marginopora vertebralis* can work to the top of a layer of coarse, shell sand 1 – 2 cm thick within 12 h. However, under conditions of extreme turbulence and continual sediment movement such as occur on the exposed, shallow shelf areas around the British Isles, the vagrant Foraminifera, like the attached forms, are limited to sheltered niches on hard substrates and in particular to the shelter afforded by 'seaweed'. In the shallow, sunlit (photic) zone the vagrant Foraminifera cling by means of their pseudopods and congregate in the 'holdfasts', especially of *Laminaria*. They similarly occur as epiphytes on *Zostera,* the eel grass, as they do on its tropical counterpart *Thalassia,* the turtle grass (Brasier, 1973, 1975a). Below the zone of macroscopic algae the Foraminifera cling to animal substrates, particularly hydroids (Dobson and Haynes, 1973) and bryozoans such as *Flustra.* They even occur on large mobile, invertebrates such as molluscs, including swimmers like scallops (Haward and Haynes, 1976).

Foraminifera living symbiotically with algae, particularly the Larger Foraminifera, are restricted to the photic zone. This may extend to only some 20 m or less in the temperate zone, but to 120 m in the tropics, before the point is reached where the products of photosynthesis can no longer balance respiration, at the respiration compensation depth (RCD). Conditions favourable for symbiosis probably disappear well before these depths; also, light penetrates only a few millimetres into the sediments.

When epiphytic and epizoic Foraminifera die they fall from their 'hosts' and accumulate in the sediments on the sea floor. Carried along by currents they become size sorted, together with the dead tests of species that live in or on the sediments. Fragile species may break down completely and robust species build up preferentially in number. Light species may be winnowed away and carried in suspension to be deposited with fine muds in quiet areas many miles from their point of origin. Even live species can be put into suspension by extreme turbulence and taken in plankton nets (Loose, 1970). It is clear that in cases like this there is no similarity between the life assemblage (biocoenosis) and the death assemblage (thanatocoenosis). The work of Atkinson (1971) shows how the numbers of dead Foraminifera in southern Cardigan Bay relate closely to the pattern of sediments. Predation may also alter the number and sizes of tests being contributed to the sediment and lower abundance by removal of individuals prior to reproduction. Worms and sponges make irregular tunnels into the test wall, gastropods make neat holes and longitudinal scrapes, while echinoderms make round holes with radiating grooves, caused by the Aristotles' Lantern (Earland, 1956; Sliter, 1971). These attacks probably contribute to the rapid breakdown of fragile tests. Further changes as a result of diagenesis would attend the transformation of the incoherent sediment into a lithified stratum in the geological column.

SUMMARY OF IMPLICATIONS FOR STRATIGRAPHY

As pointed out by Hedley (1964), the life histories of only a few species representing but a few families are known in detail. This is still true and we must recognise the force of his argument that generalisations based on this evidence may be misleading for the Foraminifera as a whole. There is also the problem that tank experiments cannot duplicate natural conditions and results so obtained must be treated with reserve. However, bearing this in mind some generalisations do appear to be possible and there are some clear implications for the stratigraphical application of the group:

(1) The ultrastructure of the soft parts and the life histories prove to be complex, matching the complication of shell structure. On the whole the distinctions that can be made support the taxonomic categories made on the basis of hard parts alone. This is important for the confident recognition of species only found as fossils. Differences in the fine structure of the pseudopods and colour of the protoplasm do not appear to be specific, but symbiotic species may associate with particular algae.

(2) The well-known dimorphism exhibited by many foraminifer species is the result of an alternation of generations. The reproductive cycle involves a diploid (B form), which after asexual meiosis produces the haploid (A form), sexual generation, as in plants. Generally the B form is larger than the A form, is microspheric and develops more chambers in multilocular species. There are variations at the specific level but the species regarded as more primitive on grounds of test structure appear to have the lowest chromosome numbers and the simplest reproduction cycles. In groups which do not

possess a true proloculus but develop a juvenarium this, like the adult test overall, is larger in the B form.

(3) Where the daughter cells and gametes are released into the open sea, as in *Elphidium,* the dead tests are vacated and left in good condition in the death assemblage, with the A forms generally much outnumbering the B forms. In species where the final chamber or chambers of the B forms are modified as brood chambers, these may be damaged or destroyed during growth and release of the embryos. The last chamber in the A form may also be modified and bear special pores for the release of the sexual gametes. These modifications must be taken into account in classification. In some cases the B forms are completely destroyed and are therefore not found in the death assemblage or as fossils at all.

(4) Under optimum conditions Foraminifera complete their reproduction cycles as soon as they reach maturity. This may be delayed, although growth continues, under adverse conditions. As the test is usually vacated after reproduction this means, paradoxically, that a large, well-grown fauna may indicate slow growth with reproduction inhibited or delayed, while a fauna of relatively small individuals may indicate favourable conditions. It is clear that faunas of small individuals occurring in the stratigraphic column should not be confused with dwarfed or 'depauperate' faunas.

(5) In life many species cling firmly to various substrates by means of their pseudopods. On death their tests accumulate in the sediment and, particularly on the turbulent, shallow shelf become current sorted along with the shells of species that live in the sediment and, perhaps, also the dead shells of planktonic species. When such faunas are encountered in the stratigraphic column they must not be confused with life assemblages. It is also possible for considerable mixing of species from different habitats to take place without marked size sorting. Apparent lack of size sorting should therefore not be taken as necessarily indicating a biocoenosis. Plainly, the use of fossil Foraminifera as indicators of past environments requires patient detective work and a thorough knowledge of their 'natural history'.

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Chapter 4

Test Morphology and Composition

> The case of the three species of protozoan ... which apparently select differently sized grains of sand, etc., is almost the most wonderful fact I ever heard of.
>
> (Darwin to Carpenter)

CHAMBER ARRANGEMENT

We have seen how the soft part biology of the Foraminifera presents certain unique features. The group is also unique among the invertebrates in the variety of test shapes and styles of chamber arrangement developed, in some cases achieving an architectural complexity that has anticipated the geodesic domes of Buckmaster Fuller. The main types are illustrated in figures 4.1 and 4.2.

The Foraminifera test is either unilocular (non-septate) or multilocular, being composed of more than one chamber and divided by septa.

Unilocular tests may simply possess an open end (or ends in branched forms) which serves as an aperture; there may be no apparent opening in some globular and hemispherical attached forms, while in others there is a definite, restricted, consistently placed opening. In the multilocular group the aperture is usually restricted and when a new chamber is added it becomes an internal foramen (plural: foramina). The foramen is often modified and different from the aperture. A tooth or teeth may be present in the aperture and in some genera the tooth is developed as a plate or tube which extends back to the previous foramen.

The chief kinds of multilocular test arrangement are as follows:

Planispiral (figure 4.2)

In this type of arrangement the series of chambers is coiled in a single plane. The chambers of each turn (whorl) may embrace former whorls (involute) or may only touch the periphery of the preceding whorl (evolute). The central area where the septal traces (sutures) meet is called an umbilicus.

Fusiform (figure 4.2)

Planispiral arrangement with the axis of coiling drawn out so that the chambers are long and low and the test is fusiform or spindle shaped.

Annular discoidal (figure 4.2)

With initial chambers planispiral and the later ones added as annular rings (concentric). The ring-like later chambers are commonly subdivided by secondary septa into chamberlets.

Annular complex (figure 4.2)

With annular discoidal 'equatorial' layer and layers of lateral chamberlets on each side, giving a generally flattened spheroidal shape.

Biserial (figure 4.1)

Chambers arranged in two alternating rows. The initial part may be trochospiral or planispiral. Planispirally wound biserial arrangement also occurs (enrolled biserial).

Trochospiral (figure 4.1)

Here the chambers are coiled in a helicoid spiral as in the gasteropod *Trochus*. The figures show the typical case where the aperture is at the basal suture on the involute underside (ventral) and the evolute upperside (dorsal) is equally raised (test biconvex).

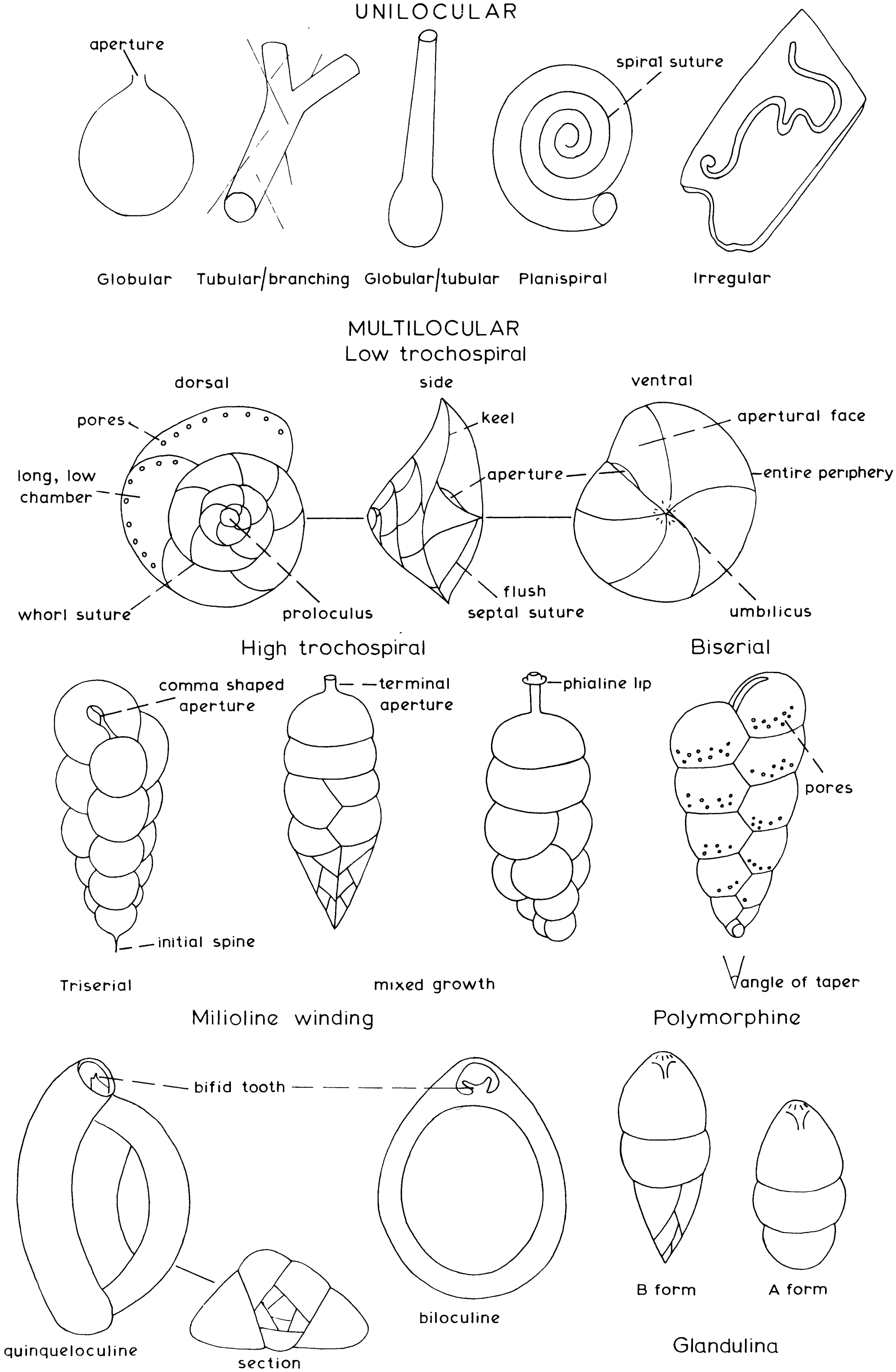

Figure 4.1 Coiling modes in Foraminifera: unilocular, trochospiral, milioline and polymorphine

High trochospiral (figure 4.1)

Trochoid genera with a very high spire exist and triserial arrangement with three chambers to the turn is particularly common. High, conical forms with annular chambers and chamberlets also occur.

Uniserial (figure 4.2)

Here the chambers are arranged in a single series, straight (rectilinear) or curved (curvilinear), the simplest form of multilocular arrangement.

Milioline (figure 4.1)

Winding growth with two chambers to the whorl with the aperture alternately at one end and then at the other. The successive chambers are added at 144° to each other (quinqueloculine), 120° (triloculine) or 180° (biloculine).

Polymorphine (figure 4.1)

Alternating growth with five chambers in each whorl added at 144° to each other, or three chambers at 120° or two at 180°. The successive chambers spiral about the growth axis of the test, all the apertures pointing in the same direction.

Other modes

Many Foraminifera also show irregular growth. This applies especially to attached forms. A small number are attached and arborescent with many branches.

Mixed chamber arrangement

Mixed or multiform growth, where the juvenile is different in arrangement from the adult chambers, is common and in some cases three different modes may be shown. Examples which appear to involve simplification include:

Planispiral to uncoiled uniserial, *Astacolus*.
Planispiral to biserial, *Spiroplectammina*.
Biserial to uniserial, *Rectobolivina*.
Trochospiral to triserial, *Eggerella*.
Triserial to biserial, *Gaudryina*.
Triserial to uniserial, *Clavulina*.

Examples which involve complication and subdivision of later chambers include:

Trochospiral to annular conical, *Patellina*.
Planispiral to annular discoid, *Archaias*.
Trochospiral or planispiral to annular complex, *Orbitoides* s.l.

These stages are normally shown more completely in the larger B form and only the final stage may be shown by the A form. For instance, in *Glandulina laevigata* (figure 4.1) the microspheric form has more chambers and is polymorphine (biloculine) in the initial part, whereas the A form is uniserial throughout and may be reduced to two or three chambers only.

It has been assumed that in multiform genera the juvenile recapitulates an ancestral adult growth stage. Phylogeny (race history) can thus be worked out from ontogenetic (individual growth) stages, shown most completely in the B form (Schubert, 1907).

According to Lecalvez (1938) the acceleration of development and lower total chamber number shown by the A form is because chamber volume is dependent on the volume of protoplasm. If the amount of protoplasm brought by the asexual daughter cell is equal to the amount carried by the first 10 chambers of the B form, then the megalosphere formed will be equal in diameter to the tenth chamber of the B form. If the B form normally develops 25 chambers then the A form will go on to develop 15. The A form then simply shows the last part of the developmental series shown by the microspheric generation which Lecalvez considered the more stable form, showing the full ontogeny. He regarded the microspheric stages as specific characters rather than a recapitulation of ancestral modes of coiling.

Support for this idea is given by details of the life cycle in *Patellina corrugata* (figure 3.4). Here, where only a few relatively large amoeboid sexual gametes are produced, the non-septate juvenarium is larger than in the A form. Nevertheless, beautiful morphological trends can be distinguished in many different groups of Foraminifera in which coiling modes first shown in both generations gradually become restricted to the B form and finally lost altogether. The microspheric generation then clearly repeats in the juvenile characters once shown more fully in the adult. In this sense many foraminiferal genera can be regarded as showing recapitulation, without this being taken to imply that the juvenile repeats

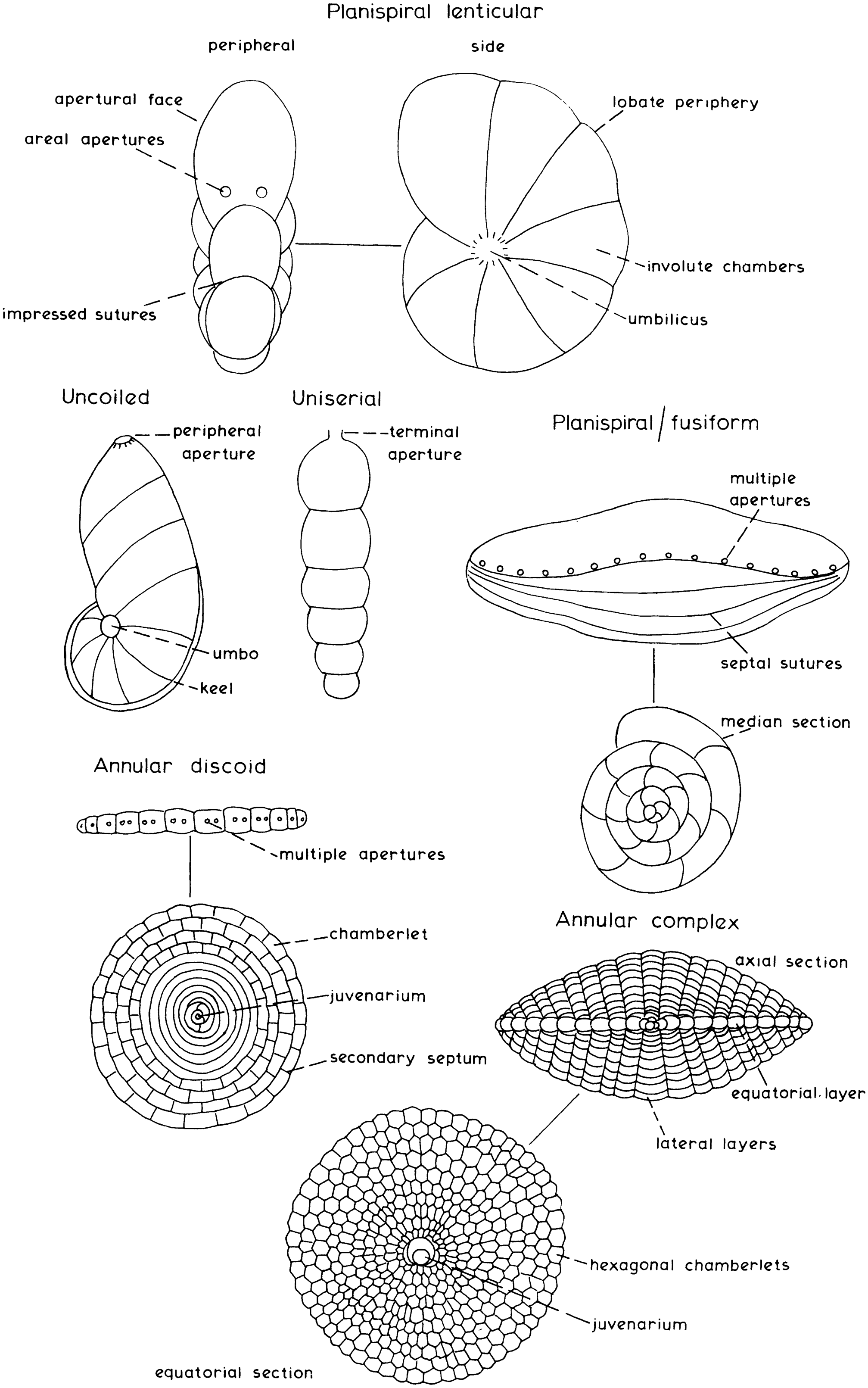

Figure 4.2 Coiling modes in Foraminifera: planispiral, uniserial, annular discoid and annular complex

all the characters shown by the ancestral forms or repeats a coiling mode regardless of its developmental and adaptive value. The stratigraphic evidence (Wood and Barnard, 1946; Cifelli and Glaçon, 1978) strongly supports recapitulation, and reversals, such as uniserial to planispiral which could be taken to support proterogenesis (evolutionary appearance of new characters in the juvenile), apparently do not occur. Nevertheless, this idea put forward by Rhumbler (1895, 1911, 1923) has been revived by Brotzen (1963) and Sellier de Civrieux (1969).

The table in figure 4.3 shows the percentages of each kind of chamber arrangement obtained from an analysis of the total fossil and recent genera of Foraminifera included in the *Treatise on Invertebrate Paleontology* by Loeblich and Tappan (1964). There are a number of difficulties in the way of accurate counts, so these are crude figures. In the case of intermediate forms and mixed growth an arbitrary decision has to be made on the grouping. No distinction is made between high and low trochospiral and regularly conical, unilocular forms. Note also that the orders recognised do not follow the 'Treatise'. It has also been thought advisable to leave out taxonomically doubtful genera. Allogromiids with partial test covering are also omitted. The imperfect nature of the fossil record must also be kept in mind. However, despite these difficulties figure 4.3 does bring out some striking statistics.

Only just over 10 per cent of the total 1110 genera are unilocular. Most of these are globular, or are spiral (dominantly planispiral) tubular forms. There are relatively small numbers of straight, tubular branching forms with open ends (apertures); tubular forms with globular initial end; and irregular forms.

Almost 90 per cent of the total genera are multilocular. Trochospiral chamber arrangement is clearly the dominant mode and low trochoid (20 per cent) and high trochoid (16 per cent) genera together make up more than one-third of all foraminiferal genera. Next in abundance are planispiral forms (15 per cent) which together with planispiral fusiform genera (8 per cent) make up

CHAMBER FORM / ORDERS	Numbers	Percent	Agglutinating	Microgranular	Porcelaneous	Hyaline	Unilocular	Multilocular	Free	Attached	Benthonic	Planktonic	Tubular Branching	Globular-tubular	Globular (inc. hemispher).	Planispiral	Conical	Irregular	Planispiral-uncoiled	Fusiform & globular	Low trochoid	High trochoid	Conical	Discoidal	Annular complex	Biserial-uniserial	Enrolled biserial	Uniserial	Milioline	Polymorphine	Irregular (inc. spreading)	Arborescent
													UNILOCULAR						MULTILOCULAR													
Total Genera	1110						11	89	93	7	95	5	1	<1	4	4		1	15	8	20	16		5	2	6	1	4	5	2	4	<1
Astrorhizida	81	7	25				100	0	67	33	100	0	18	9	51	13	2	9														
Lituolida	215	19					0	100	95	5	100	0							19	<1	7	35	5	8		10		6	4		5	
Fusulinida	138	13		13			6	94	95	5	100	0				6			21	49	2		3			5	2	5			5	
Miliolida	144	13			13		11	89	92	8	100	0			<1	8	1	3	27	9	2		3	7					33		5	
Nodosariida	84	8				49	7	93	90	10	100	0			7				17							7		29		30	10	
Buliminida	97	9					0	100	100	0	99	?1									2	70				17	10	1				
Robertinida	36	3					0	100	100	0	100	0							7		86	7										
Rotaliida	256	23					5	95	91	9	100	0				2	2		18	1	40	1	5	8	14	2					4	2
Globigerinida	59	6					1	99	100	0	0	100			2				21	7	50	7				8					5	

Figure 4.3 Coiling modes in the main groups of Foraminifera analysed by genera. Numbers based on the 'Treatise' (Loeblich and Tappan, 1964). Note that there have been subsequent increases in all groups

one-quarter of all foraminiferal genera. Biserial (to uniserial) arrangement (6 per cent), annular discoidal (5 per cent) and milioline winding (5 per cent) are less abundant and the other modes including uniserial, enrolled biserial, annular complex, polymorphine and irregular are less than 5 per cent, with the arborescent mode less than 1 per cent. Of course, these figures give no idea of the relative abundance of the different genera and species. For instance, it is largely the fusiform, annular discoidal and annular complex, Larger Foraminifera that are responsible for the foraminiferal limestones. However, the figures do give a good idea of the preferred coiling arrangements at the generic level which, we can assume, must relate to the different life 'strategies' of the Foraminifera (see below).

COMPOSITION AND STRUCTURE OF THE TEST WALL

There are three basic kinds of test wall. In the first, the test is formed by an organic membrane composed of tectin (a proteinaceous mucopolysaccharide—that is to say a complex carbohydrate plus protein) in the form of a soft film (Hedley, 1964). In the second group, this membrane becomes the foundation for an agglutinated wall and, in the third, the inner lining for a calcareous wall (Banner and Williams, 1973; Poignant and Rouvillois, 1978).

The test in the membranous group (Allogromiids) is unilocular, thin and flexible. Hedley (1964) has shown how *Shepheardella* and *Allogromia* can change their shape very rapidly. A number of these naked genera, such as *Neogullmia*, live inside the dead shells of other Foraminifera and in worm tubes, while others like *Myxotheca* develop a partial agglutinated covering or a ferruginous encrustation, as in *Kibisidytes*.

In detail, the structure of the membrane appears to be quite complex, consisting of a spongy, possibly fibrous, network in *Shepheardella* (Hedley, Parry and Wakefield, 1967) and laminated in *Myotheca* with the fibres of one layer laid down at right angles to those of adjacent layers (Angell, 1971). Different species of *Allogromia* have also been shown to have differences in the fine detail of the wall (Hedley, Ogden and Wakefield, 1972).

Agglutinated Wall Structure

There is a gradation from genera with adventitious material loosely attached to the organic membrane, such as *Rhizammina*, to strongly built genera where the grains are held firmly with calcareous or ferruginous cement such as *Eggerellina*. Many genera such as *Astrorhiza* are not selective and make use of the available material of the sea bed indiscriminately, including sand grains, sponge spicules, mica flakes, coccoliths, diatoms and heavy minerals.

Others are selective of particular kinds and sizes of materials, in particular: sponge spicules in *Technitella legumen*, arranged in a two-layered warp and weft pattern, echinoderm plates in *T. thompsoni*, the dead tests of other Foraminifera in *Reophax testacea*, mica flakes and needles of rutile in *Bathysiphon argenteus* (Dick, 1928). A possible example of selection of extra-terrestrial microtectites has been reported by Baker and Glass (1974) in *Rhabdammina* and *Gaudryina* from deep sea sediments of Eocene age in the Caribbean. Although abundant in the sediment the microtectites selected are generally larger than the rest of the agglutinated material and usually centrally placed on the test. More commonly calcareous or arenaceous grains are built flat on to the wall surface with the large grains characteristically packed in a matrix of smaller grains (Haynes *et al.*, 1973; Murray, 1973a; Towe, 1967).

Although larger grains may be used as growth proceeds, the size range may be specific. Thus Lipps (1973) found that *Trochammina pacifica* consistently incorporates finer sized material than *Miliammina fusca*, although these species live together on marshes at Bodega Bay, Northern California. Similarly, on the Dovey marshes, Wales, *Miliammina fusca* consistently builds its test of relatively large silt grains, while *Trochammina inflata* is constructed of very minute grains averaging about 3 μm in diameter (plate 7, no. 8). Many species show selection of material of a particular size and shape for a particular purpose (Haynes *et al.*, 1973). Thus *Lagenammina* cf. *hancocki* shows selection of small-sized grains for the apertural rim (plate 7, no. 9) and *Ammobaculites balkwilli* has sharp silt grains set up on end around the aperture. *Halyphysema tumanowiczii* has sponge spicules jutting out at an angle from the head and apertural end. *Saccammina spherica* var *anglica* builds its test on a tripod of spicules.

As pointed out by Lipps (1973): 'the biochemistry of the organic linings or cements of agglutinated foraminifera remains largely unknown', and what is thought to be known is surrounded by controversy. Hedley (1964) considered that the organic linings were equivalent to the tectin membrane of the allogromiids but the variation that probably exists is indicated by the discovery of a collagenous, fibrous sheath in *Halyphysema* (Hedley and Wakefield, 1967) together with an acid, mucopolysaccharide cement.

In the majority of agglutinating forms (perhaps all genera) the cement is mixed with organically bound iron (Hedley, 1963; Towe, 1967; Murray, 1973a) which on oxidation hardens the test and gives it a red-brown colour. The last-formed chamber may be white but Hedley found that the cement in this part and in white shells contains equal amounts of iron. In a number of genera from normal marine environments the cement is also mixed with considerable amounts of calcium.

Although ferric granules appear in the cytoplasm of both *Haplophragmoides* and *Rhabdammina*, Hedley still considers that the ability of Foraminifera to secrete iron is unproven. Lipps considers that there is no direct evidence that the agglutinating forms secrete calcium either and that both iron and calcium may become bound in the organic cement by inorganic processes.

Formerly, a number of agglutinating forms were considered to possess siliceous cement (Rzehakinidae) because their tests did not dissolve in acids. However, Lipps (1971) has shown that the tests of this group disaggregate in hydrogen peroxide, indicating that the siliceous grains of the tests are held in an organic cement. These results have been confirmed by Hansen and Hanzlikova (1974) by electron microscopy, electron microprobe and X-ray diffraction studies. Again, no evidence of siliceous cement was found, although sutured areas indicating diagenetic welding of the siliceous grains in fossil species was observed.

Calcareous Wall Structure

Very early in foraminiferal studies the major groups of calcareous genera were distinguished as porcelaneous or glassy according to their appearance in reflected light. Thus in the porcelaneous group the wall may resemble porcelain with a shiny white surface that results from a fine structure that leads to maximum reflection of light. On the other hand the glassy group have a fine structure that readily allows light to pass through, so that some of these genera resemble clear soap bubbles or blown glass. Crystallographic investigations were started by Sorby (1879), continued by Sollas (1921) and taken up with such affect by Wood (1949a) that for three decades they have been a major area of research and the results the basis of modern classification of the Foraminifera.

Porcelaneous

The white, porcelain-like group of calcareous genera studied in thin section and in isolated fragments by Wood were found to be built of a random array of calcite laths exhibiting first-order grey, interference colours under crossed nicols. Some areas of the wall showed preferred orientation, and further studies by TEM (Lynts and Pfister, 1967) and SEM (Haake, 1971; Cherif and Flick, 1974) have shown that generally the wall is composed of three layers: a thick median layer of laths in random array with thin inner and outer veneers (figure 4.4). In smooth, shining species the laths in the surface veneer are arranged parallel to the surface, in a 'tile-roof' 'or parquet-floor' pattern (plate 7, nos. 1, 2). In rough-walled species such as *Quinqueloculina berthelotiana* the laths of the external veneer are arranged perpendicularly to the surface to give a cobble pattern. The laths of the inner veneer appear to be parallel to the surface in both cases.

In transmitted light, porcelaneous walls show a characteristic rich brown coloration. This appears to be due to included organic matter, the organic 'moulage' of Arnold (see below).

Microgranular

An important group of calcareous Foraminifera occur in the Upper Palaeozoic and as they have a dark wall which sometimes includes agglutinated grains they were considered by the early workers to belong to the agglutinated group. This view was followed by Cushman (1948) who considered the wall was composed of adventitious material bound by a calcareous cement. On the other hand, Plummer (1930), Galloway (1933) and Rauzer-Chernousova (1936) considered the wall could have been secreted by the animal itself.

In large part the difficulty workers have had in interpreting the structure is because the wall is commonly recrystallised. However, detailed work by Wood (1949a) and Cummings (1955, 1956)

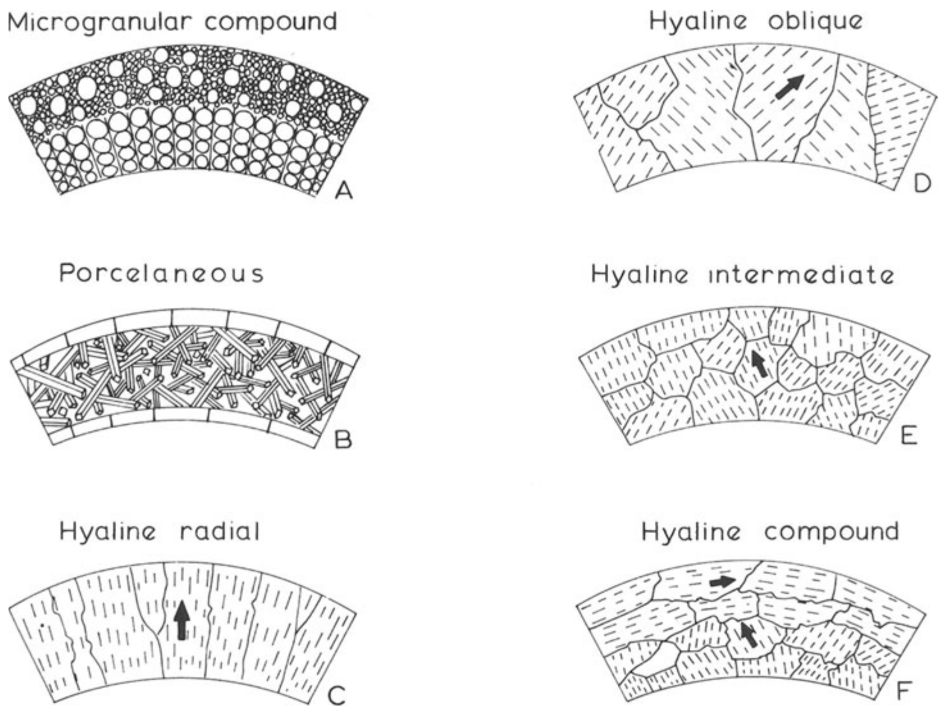

Figure 4.4 The main types of secreted, calcareous walls

showed that the wall is formed of equidimensional, subspherical granules of calcite closely packed together but without detectable cement. It is commonly compound with an outer layer of irregularly packed grains and an inner layer of granules arranged in orderly rows perpendicular to the test surface, as in *Palaeotextularia* (figure 4.4A). As pointed out by Cummings, this linear arrangement of grains produces a light and dark 'fibrous' appearance as seen in thin section. There is apparently no preferred orientation of the c-axes and the structure is quite distinct from that of the hyaline group.

Hyaline or glassy

Two major types of hyaline wall were distinguished by Wood (1949a, 1963) on the basis of optical characters observed in thin sections or fragments under crossed nicols of the polarising microscope. These are first, radial structure, characterised by, 'a black cross with concentric rings of colour closely mimicking a typical (negative) uniaxial interference figure. The test is built of crystals of calcite with their c-axes normal to the spherical surface'. The second structure showed no extinction pattern but, 'a multitude of tiny flecks of colour, and in section their structure is seen to be minutely granular'.

Further work by TEM (Towe and Cifelli, 1967; Hansen, 1970a; Stapleton, 1973), X-ray diffraction (Hansen, 1968) and SEM (Hansen and Reiss, 1971; Bellemo, 1974a, 1974b, 1976) has shown that in both cases the test is built of units composed of numerous platelike or rhomboidol crystals each about 1 μm in diameter. These units are enclosed in an organic membrane and irregularly sutured together. The difference in optical characteristics is caused by growth of the crystals preferentially on the basal pinacoid (0001) crystal face in the radial type, whereas in the type considered 'granular' by Wood growth is preferentially on one of the rhombohedral faces (1011). In the radial type the rhomboidal microcrystals are stacked in columns which extend fully across the wall (figure 4.4C) and the c-axes are perpendicular to the surface with only minor deviations. In the 'granular' type the stacks of microcrystals extend obliquely across the wall (figure 4.4D) and the c-axes incline at 5° (Stapleton, 1973). Adjacent units may incline in different directions because of rotation of the stacks of crystals (Bellemo, 1974b), but the c-axis is never perpendicular to the test wall. For this reason none is seen to extinguish when pieces of test wall are examined under crossed nicols which then appears to be built of randomly orientated grains.

The difference between radial and oblique microstructure is dramatic when seen through the polarising microscope (plate 7, nos. 3,4), but as Towe and Cifelli (1967) point out they are crystallographically very similar and one could easily give rise to the other. Mixed types do occur and Bellemo (1974b) has shown that the wall in species such as *Cibicides refulgens* and *Cibicidella variabilis* which has been found difficult to interpret (Wood and Haynes, 1957) and described as indistinctly radial by Towe and Cifelli, is actually of intermediate type (figure 4.4E). The crystal units are small and do not extend fully across the wall. In the inner and outer zones the c-axes are almost perpendicular to the test surface, while in the middle they are more oblique, about 60°. Compound structures also occur in *Cibicides lobatulus* and *C. floridanus*, where the inner layer of the two-layered wall is of intermediate structure while the outer is composed of units of crystals with the c-axes parallel and the a-axes perpendicular to the test surface, as in figure 4.4F (Bellemo, 1976; Towe, Berthold and Appleman, 1977). Similar mixed structures occur in *Lepidocyclina* and *Miogypsina* (Ouda and Sharara, 1978).

An interesting and unusual structure occurs in the Spirillinidae, considered by Wood (1949a) to have tests constructed of a single crystal. This observation has been confirmed by X-ray diffraction and crystal overgrowth techniques as well as polarised light microscopy (Towe, Berthold and Appleman, 1977), which show that *Patellina corrugata* behaves as a single crystal of calcite with the c-axis parallel to the base of the conical test and the a-axis parallel to the axis of the cone. Individual plates and spines of echinoderms are single crystals but this group of Foraminifera are the only organisms known in which the entire skeleton is a single crystal.

A small but important group of hyaline Foraminifera are built of aragonite rather than calcite (Troelsen, 1955; Todd and Blackmon, 1956; Vénec-Peyré and Jaeschke-Boyer, 1978). A recent example is *Hoeglundina* which is common in cool, deep water and possesses a beautifully glassy wall seen in reflected light. *Epistomina*, an allied form abundant in the Mesozoic, is often found as a cast with the test partially dissolved away. This is because aragonite goes into solution more readily than calcite on fossilisation.

Aragonite crystallises in the orthorhombic system but pseudohexagonal twins are commonly formed. These have been shown to occur in the wall of *Hoeglundina*, arranged with the basal pinacoids parallel to the test surface. The crystals are optically biaxial but the angle is so small that extinction under crossed nicols resembles that of the radial, calcitic forms (Reiss and Schneidermann, 1969).

Fine Structure of the Wall in Hyaline Foraminifera

Thin sections of glassy Foraminifera studied both by light and electron microscopy show that not only are many tests layered with compound wall structures but that generally they are lamellar, as originally discovered by Williamson (1852). This means that when a new chamber is added a layer (or layers) of calcite extends back to cover the previously formed test (Smout, 1954; Hansen and Reiss, 1971, 1972a; Grønlund and Hansen, 1976). The main kinds that have been distinguished are shown in Figure 4.5A – F.

In the agglutinating, porcelaneous and microgranular groups, when a new chamber is added to the test it simply abuts the previous chamber, as in A. Although nonlamellar structure also occurs in the hyaline group, lamellar investment is a general feature. Monolamellar structure, where each chamber is composed of one layer, either fully developed as in B, or partial as in C, is characteristic of the nodosariids. Multilamellar structure, where each chamber has several primary layers, also occurs, as in D.

In the other groups of hyaline Foraminifera, including the aragonitic genera, bilamellar structure appears to be general. The chamber wall has a basic construction of two layers separated by a membranous 'median layer' or 'primary organic membrane' (POM of Hemleben *et al.*, 1977), and it is the outer layer that extends back over the previously formed test, as in E.

A number of genera show a further complication in that the inner layer coats the apertural face of the previous chamber to a greater or lesser extent, as a septal flap, shown in F, often modifying the internal foramen and giving rise to a tooth plate.

The outer lamella gives rise to ornament of spines and ribs by localised thickening, and the presence of an external layer of protoplasm capable of laying down a complete lamella of calcite over the previously formed test explains how ribs and keels can be formed running its entire length.

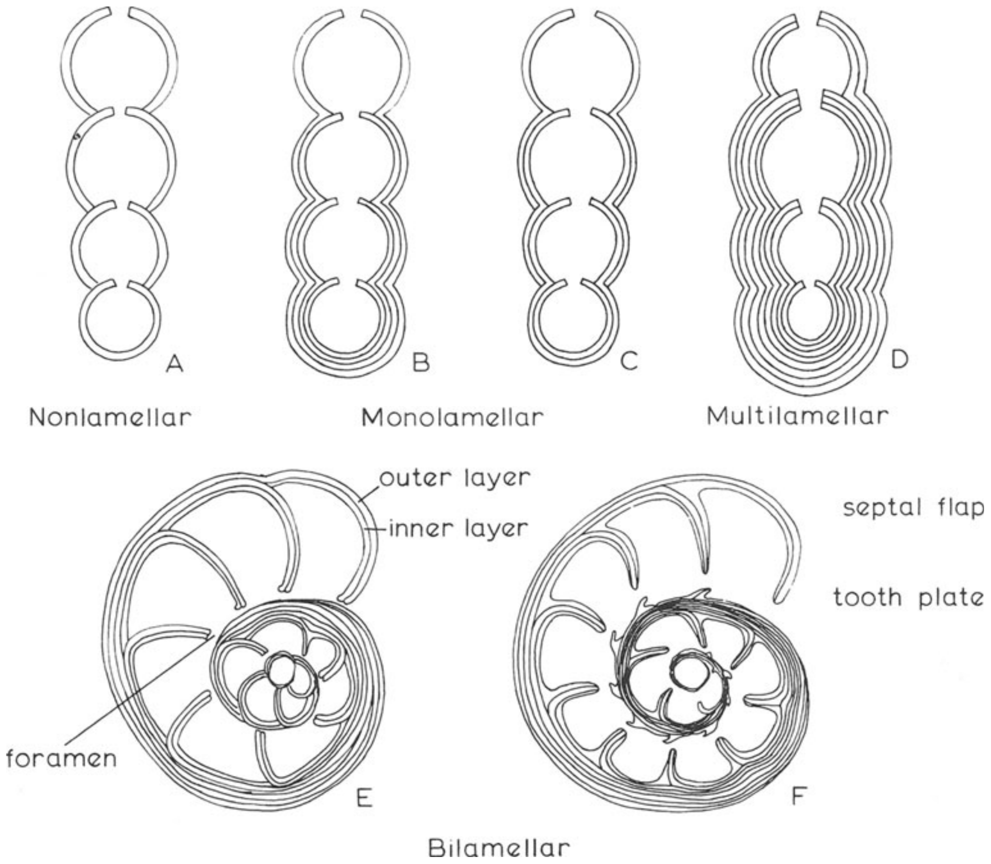

Figure 4.5 Sections showing various types of lamellar wall structure in the hyaline Foraminifera (idealised). A – D uniserial nodosariids: A nonlamellar, B lamellar and fully investing, C partially lamellar, D multilamellar. After Grønlund and Hansen (1976). E and F equatorial sections of low trochospiral or planispiral rotaliids: E bilamellar, F bilamellar with septal flap

Perforations

The walls of hyaline Foraminifera are usually perforated (plate 7, no. 5). Pores also occur in the microgranular group and more rarely in certain agglutinating genera, but are absent in the porcelaneous Foraminifera. In perforate genera, the walls between the chambers (septa) and external ridges and keels remain imperforate. Externally the pores appear round to oval or slit-like and the opening on the inside of the test is usually larger and funnel shaped. They may be restricted to particular zones and be of different sizes in the same individual, although the range may be constant for the species. Large ones may occur only on one side in trochospiral species.

The organic membrane is imperforate but Arnold (1954a, 1954b) and Angell (1967) have shown how it is thickened at the base of each pore, this 'pore plug' being microporous. The pore is also lined with a membrane that appears as an elongate tubule in etched specimens (Jahn, 1953; Banner and Williams, 1973). Although occasionally interrupted, the pores normally continue through the successive lamellae giving a 'fibrous' appearance to hyaline tests. Calcareous plates which are also perforated (sieve plates) may be present at the junctions or 'nodes' representing calcification of the organic membranes. The pore plug may also be calcified.

GROWTH OF THE TEST

Test construction in Foraminifera appears to take place within a protective cyst, so observation is difficult and is limited to a few species. The pseudopodia are active both in the construction of the cyst and in the building of the test which begins with the formation of the tectin lining. The process was well described by Jepps (1942), and it is worth while quoting in full her description of the growth of a new chamber in *Elphidium crispum*:

> An unusually dense fan-shaped mass of closely-set anastomosing pseudopodia make their appearance, radiating out from the terminal apertures of the last chamber of the shell. Beyond them bundles of ordinary pseudopodia may reach out farther to collect any material that may be available (diatoms, excretory granules, sand, etc.) to make into a 'face-mask', inside which the new chamber will be formed. But the process can go without this cover.... Activity usually begins in the late afternoon or early evening, the protoplasm, which may be withdrawn at the time from the last chamber, passing out in the form of pseudopodia which flow through the successive sets of foramina, and also emerge at the fossettes and pores at the sides of the last chamber which will be partly covered by the new one. Some of the special pseudopodia after a time begin to arch over in a reticulum which outlines the cavity of the future chamber, usually about 10 p.m. to midnight, the 'face-mask', when present, being pushed away to the outside. They gradually swell at their bases and merge into one another there, whilst a fluid wells out amongst them and comes to fill up the space they enclose under their extremities with a uniformly granular mass of colourless protoplasm in which the pseudopodial streams fade out and ultimately disappear into the general circulation of the mass. This comes to have a clear-cut surface, fashioned in the shape of the new cavity even to the retral processes and the projections at the future foramina.... The longer and more active pseudopodia which normally collect the 'face-mask' material have disappeared, and the short pseudopodia remaining at the surface of the protoplasmic mass now appear stiff, with very sluggish movements. They may come and go, as the shell is deposited on the mass; it is impossible to know how much of their variation under observation is due to unnatural illumination, etc., but in any case the shell seems to be porous from the beginning, and therefore, bathed in protoplasm which lays it down initially and may continue to add to it (and at times to reabsorb it) throughout life. As soon as the surface is available a collection of shining granules may be seen there which gradually form a thin layer of shell. This seems to be laid down in patches like the pieces of a jigsaw puzzle, which unite, losing their separate outlines more or less completely as the shell thickens. After a time the characteristic tubercles are formed on the outside and the keel is laid down at the periphery. During the next day the *Polystomella* remains immobile, while the shell is deposited. There is a flow of brown protoplasm into the now penultimate chamber and sometimes into the base of the new one. Then the colourless mass there becomes vacuolated and may be withdrawn altogether, leaving the new chamber empty for a time, as is usual during the greater part of the life of a *Polystomella*. Pseudopodia emerge, the 'face-mask' is cast off, and the *Polystomella* moves away to begin feeding again some 24 hours after the emergence of the protoplasmic mass.

This process was observed to take about 8 h for completion. Of particular interest is the observation that the pseudopods appear to be responsible for the secretion of calcite and that calcification is patchy and resembles the pieces of a jig-saw puzzle. It is noteworthy that Towe and Cifelli (1967) use this same simile when describing the sutured units of microcrystals observed by TEM in *Lenticulina calcar*.

The process appears to be rather different in the porcelaneous group. The growth of a new chamber in *Spiroloculina hyalina*, as described by Arnold (1964), involves mineralisation of a thick organic 'moulage' with an internal wall of 6 μm. Mineralisation begins in the central area with formation of crystals on the internal wall which build up into hummocks and ridges that gradually coalesce and spread over the test wall, eventually reaching the aboral and oral areas. There may be several waves of mineralisation before the organic matrix is completely calcified.

Further observations of growth in the hyaline Foraminifera have been made by Angell (1967). During chamber formation in *Rosalina floridana* the organic lining of the new chamber was seen to be secreted by the pseudopodia. It is a two-layered structure composed of a thick mat of fibres with a fine outer layer of beaded fibrils. The thick inner layer also coats the inside of the chambers of the previously formed test each time a new chamber is added. The inner lining of the test is therefore laminated and thickens towards the proloculus.

Towe and Cifelli (1967) have suggested that the organic membrane serves as a template that determines the orientation of crystal growth

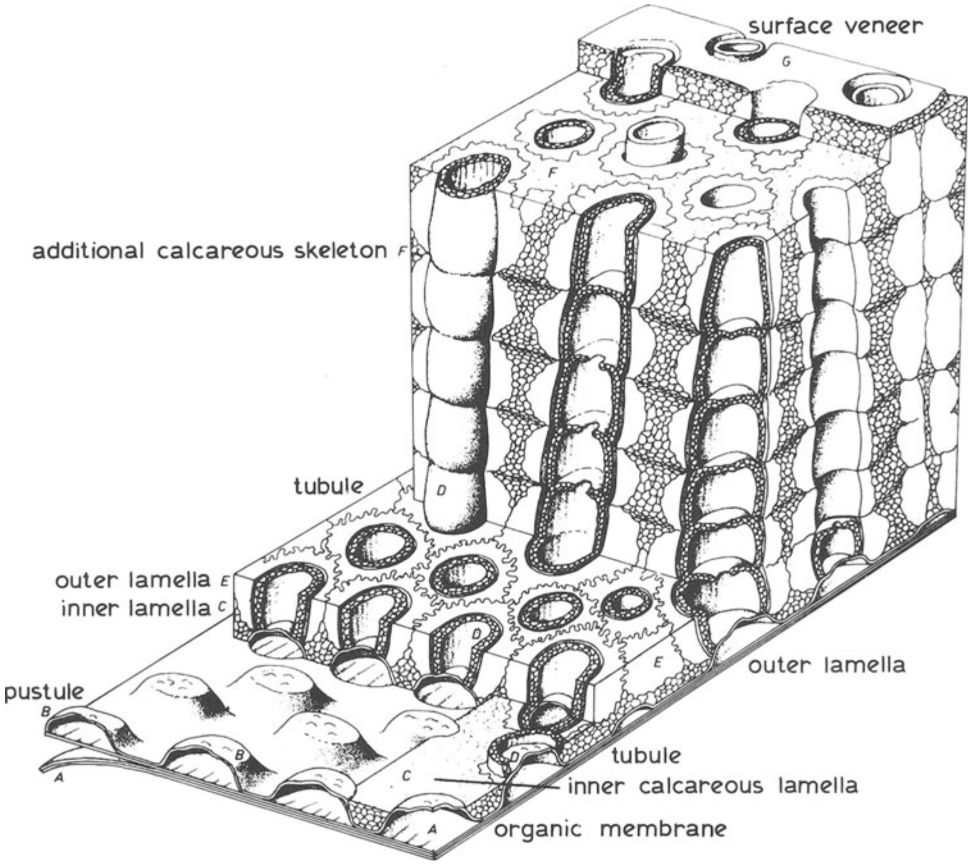

Figure 4.6 Detailed structure of the wall in *Ammonia*. After Banner and Williams (1973)

(epitaxy) or that calcification takes place in organic compartments. However, they admit there are a number of weighty objections to either hypothesis, including failure to explain the preferred orientations in the hyaline group.

Although Angell was unable to observe calcification in *Rosalina floridana* the new chamber, prior to this process, is filled with a gel-like, vesicular protoplasm. This flows out on to the outer surface as dense cytoplasm flows in from the penultimate chamber to replace it. Lipps (1973) suggests that nucleation of crystals may take place on the organic membrane and that their three-dimensional growth is supported by the gel-like ectoplasm.

In an attempt to explain the structures found in several species of *Ammonia*, Banner and Williams (1973) postulate the following sequence in wall construction (see figure 4.6):

(1) Formation of 'chitinoid' organic membrane with pustular outer lamina, A and B.

(2) Deposition of calcareous granules (rhomboid microcrystals of Bellemo) around the pustulae to form the inner lamella, C.

(3) Formation of tubules with calcareous granules incorporated in cylindrical tectin sheets, D.

(4) Tectin secreted around tubules and over inner lamella (median layer of Hansen, Reiss and Schneiderman, 1969).

(5) Deposition of sutured units of 'blocky grains of calcite' around the tubules as the framework of the outer lamella, E, with additional granular 'calcareous skeleton' between, F.

(6) Deposition of thin surface veneer of smaller granules protected by a tectin outer coat which also covers the tubules, G.

Subsequently, as new chambers are added, extra outer lamellae build up on this essentially bilamellar structure. The tubules are added to lengthwise, each new section being built on the perforate roof of the previous section and marked by a constriction. Again, as each new chamber is added an extra lamina is added to the 'chitinoid' inner lining.

In contrast to this idea that the inner lining is the first to be formed, Hemleben *et al.* (1977) on the basis of their studies of *Globorotalia cultrata* regard the median layer as the 'primary organic membrane'. They believe that calcification starts with the simultaneous secretion of the inner and outer calcite lamellae on either side of the POM. These calcite layers are in turn bounded by inner and outer tectin membranes formed by the inner and outer cytoplasm. Their observations also indicate that the incipient wall is calcified before the pores appear. Micropores appear first, on the site where the pores are eventually formed by resorption. The wall apparently remains flexible during the early stages of calcification. Individual crystallites appear surrounded by organic material. These are granules at first, but later become euhedral.

The view that the inner lining does not act as a template for subsequent calcification is supported by the work of Spindler (1978b). In *Heterostegina* it develops some days after chamber formation is complete, starting beneath the pores. It also appears to be missing in the youngest chamber.

It will be seen that in the multilocular Foraminifera, growth is episodic. This led Smout (1954) to consider each episode of chamber growth as a separate 'instar'. In tubular, unilocular genera growth may be more or less continuous. Growth in spherical, unilocular genera is believed to involve continuous rebuilding of small sections of the wall (Glaessner, 1945; see reprint, 1963a), but as both *Iridia* and *Saccammina* are known to vacate their tests and build completely new ones (Hedley, 1962) it may be that both agglutinating and calcareous genera produce a series of true instars during growth.

FUNCTION OF THE TEST

The Organic Membrane

In the 'naked' allogromiids the test is restricted to a membranous envelope which is all that stands between the foraminifer and the external environment. Transport through the membrane appears to be only by osmosis and as well as controlling exchange with the exterior it acts as a protective shield against external physical and chemical changes.

Calcium carbonate is normally soluble in oceanic water, so calcareous forms require the protection of the inner lining and the external tectin membranes that coat each lamella (Banner and Williams, 1973), particularly in waters of low pH or undersaturated in carbonate. The efficiency of the membranes as a protective device is revealed by Bradshaw's experiments on *Ammonia tepida* (Bradshaw, 1961), which show that even if the calcareous outer wall is dissolved by acid the foraminifer can survive, protected by its membranes, and build a new calcareous shell. The aperture and foramina may also be closed off by membranous partitions in unfavourable environments (Arnold, 1967).

In perforate genera the pores are lined and plugged with organic material. Cytoplasm has been noted within the pores and it is thought that small particles can enter and leave after filtering through the perforated plugs and sieve plates (Arnold, 1954a; Towe, 1971; Sheehan and Banner, 1972). However, Berthold (1976) considers their function to be osmoregulation, gas exchange or the intake or excretion of dissolved organic substances. It now seems certain that the sieve plates are too fine to allow pseudopods to pass through the pores. In many cases, when live Foraminifera are treated with reagents such as rose Bengal only the protoplasm in the ultimate and penultimate chambers stains which suggests that the pores in the earlier chambers may be permanently closed off. That the foraminifer exerts control over this process is shown in *Tretomphalus* where the pores, in the free-floating planktonic stage, are sealed by a pigmented membrane, apparently to prevent escape of the gametes (Myers, 1943b).

As well as protecting the foraminifer against chemical changes in the sea water the organic membranes, particularly the 'chitinoid' inner lining of many genera, may act as a light filter, excluding the oxidising and metagenic shorter wave lengths while transmitting the range suitable for photosynthesis by algal symbionts (Banner and Williams, 1973; cf. Haynes, 1965).

The importance of the organic membranes is underlined when in addition to their primary protective function we consider that, as has been seen, they are the foundation for the construction of the agglutinated test and of the secreted calcareous test.

The Hard Shell

The simplest type of agglutinated test is a low dome or tent-like structure, as in *Iridia,* or a subspherical mass of agglutinated grains, as in *Psammosphaera*. These probably developed from the partial, agglutinated coverings which occur in genera such as *Myxotheca* which may have arisen as an attempt to control buoyancy (cf. Marszalek, Wright and Hay, 1969). As shown by figure 4.3,

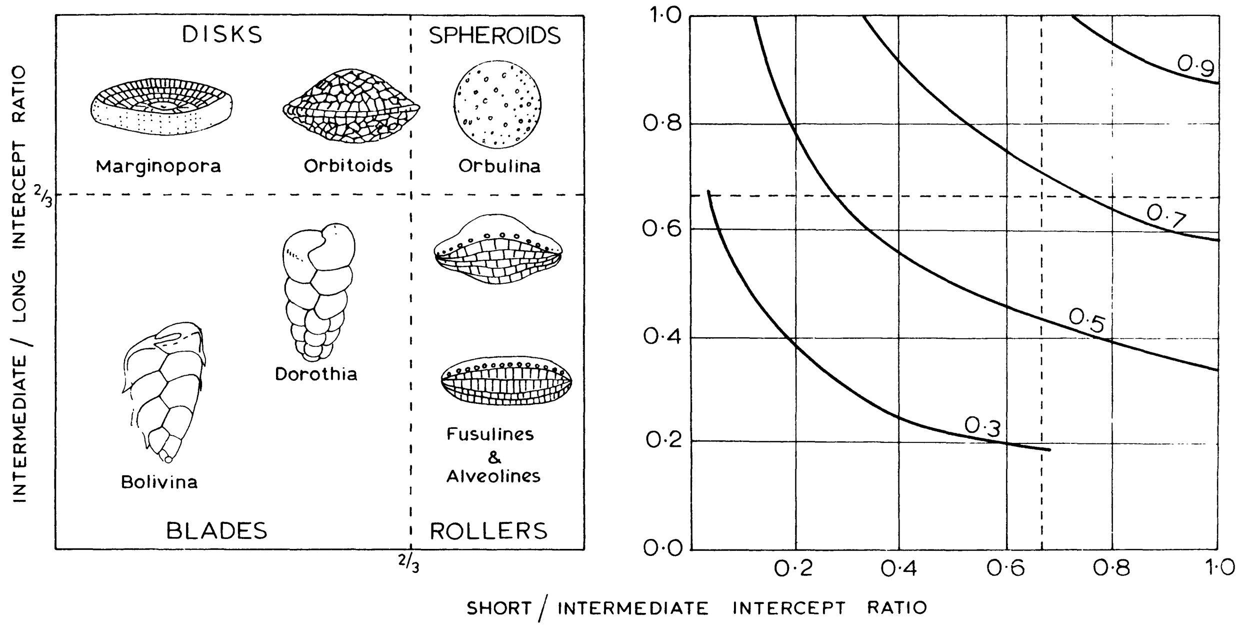

Figure 4.7 Shape classification of Foraminifera based on ratios of intercepts, the ratio of intermediate to long intercept plotted against the ratio of the shortest to the intermediate intercept. This gives the four shape classes shown on left. On the right, lines of equal sphericity are plotted as curves on the same diagram. These are derived from the equation for measuring sphericity which considers the object relative to an enclosing sphere. The sphericity of the object increases as it occupies more of the circumscribing sphere. When the two volumes coincide the sphericity is 1.0. Krumbein and Sloss (1953)

slightly more than half of the unilocular agglutinating genera are globular or hemispherical forms, with almost equal numbers of these being attached or free. A general tendency towards restriction of the aperture indicates the protective function of the complete, agglutinated covering. Approximately 13 per cent are enrolled, demonstrating the advantage of a compact test for free, wandering forms. The adoption of a hard test meant the inevitable loss of flexibility so well shown by many allogromiids. However, it is possible that some simple agglutinated forms could build a range of test shapes (Hedley, 1964).

As noted, some 90 per cent of the hard-shelled Foraminifera are multilocular. The peculiar advantage of the multichambered form indicated by this high percentage has been explained by Marszalek *et al.* (1969) as due to the extra protection afforded by the constricted chain of apertures and internal foramina which checks density currents and diffusion processes and allows time for osmoregulatory adjustment. When the pores of perforated genera are sealed by organic plugs and membranes, the test is then an effective barrier against changes in osmotic pressure and water chemistry. It is noteworthy in this regard that the endoplasm is commonly restricted to the penultimate chamber.

The strikingly different modes of coiling in the multilocular Foraminifera are considered by Lipps (1975) to be related to different feeding strategies. This is because feeding habits affect the deployment of the pseudopods and may dictate test structure. Lipps distinguished four main groups:

Suspension feeders. Erect tubular, often branched forms fixed to the sea bed or embedded in sediment and spreading their pseudopods in the water column. Common in quiet conditions, as on the abyssal plain.

Detrital scavengers. Active lenticular forms on soft substrates or in weed and elongate forms passively feeding near the sediment/water interface.

Herbivores. Largely trochoid or flattened forms browsing on algae on various substrates as active vagrants or fixed temporarily with the pseudopods streaming in all directions.

Carnivores. Active or passive forms with diverse morphologies like *Astrorhiza,* which is a passive carnivore that extends its pseudopods into the sediment to prey on minute, interstitial animals (see Buchanan and Hedley, 1960).

Lipps emphasises that the different strategies are not adapted to particular food types and that most species are opportunistic, omnivorous, feeders. Also, as we have seen in chapter 3, many Foraminifera appear to require a mixed diet. This means that a particular coiling mode may allow exploitation of more than one feeding strategy. However, the 'striking correlation' recognised by Bandy (1960a) between test structure and composition of Foraminifera with environment (broadly with temperature and depth) strongly supports the idea that the different coiling modes are adaptive and that their repetition in the major groups is the result of evolutionary convergence.

Although research is only at the beginning in this field, and is still largely speculative, it is worth while to examine the frequency of the different coiling modes (figure 4.3) and relate them to feeding strategies as well as environmental and hydrodynamic factors (figure 4.7).

Tubular branching and arborescent forms make up about 2 per cent of the whole and are practically confined to the Astrorhizida (27 per cent) and Rotaliida (71 per cent). The majority of the tubular astrorhizids, including numerous fragile genera, occur in the deep sea in soft ooze, a sediment that is largely built up from fine organic material dropped from suspension. The arborescent rotaliids are more strongly built and attached to hard substrates in current swept conditions, as in the wave zone and in reefs. In both cases these forms are well adapted to live as suspension feeders although a stellate, branching, tubular form is also consistent with carnivorous feeding in *Astrorhiza* and possibly also with detrital feeding in other cases.

Lenticular, planispiral genera, which Lipps supposes are adapted to active detrital feeding and bacterial scavenging, are much more abundant and make up some 18 per cent of all genera. In particular they make up a high proportion of miliolids (27 per cent), fusulinids (21 per cent), lituolids (19 per cent) and nodosariids (17 per cent). This coiling mode is consistent with an active life both as a browser in weed and as a deposit feeder on soft substrates. It is exemplified by *Elphidium macellum* which is abundant in the littoral algal zone. The compressed test is hauled along by the pseudopods in a semi-upright position and the juveniles have a spinose keel which helps them to lodge in the algal fronds. The peripheral keel commonly developed in these lenticular forms, especially in the nodosariids such as *Lenticulina*, may help to stabilise the test on soft substrates.

Elongate genera, which Lipps supposes are adapted to passive deposit feeding near the sediment/water interface, are equally abundant and if high trochospiral/uniserial, biserial/uniserial and uniserial are grouped together make up some 25 per cent of all genera. These modes are dominant in the lituolids (56 per cent), buliminids (87 per cent) and in the nodosariids (36 per cent). This figure reaches 66 per cent in the nodosariids if polymorphine coiling (30 per cent) is also included.

Elongate, quinqueloculine coiling is also associated with an infaunal feeding strategy in *Miliammina*, allowing it to move easily below the surface. Here the terminal aperture directs a podostyle of pseudopods into the sediment (Frankel, 1975). It may be that the remarkable tendency for chamber reduction and development of uniserial chambers with terminal apertures (often produced and with tooth plates) seen in so many lines of Foraminifera is the result of convergent adaptation to this feeding strategy. The observation that benthonic food resources are concentrated at the sediment/water interface and in the top 5 cm of sediment is very significant in this context (Walker and Bambach, 1974). The flattened, shovel shape of many species of *Biloculinella* may also have originated in the same way. However, chamber reduction with a return to a unilocular adult form occurs in *Fissurina* and *Lagena* which are parasitic upon other Foraminifera (Lecalvez, 1947; Haward, 1977). But whereas the aperture appears to be developed as a probe in *Lagena*, in *Fissurina* the aperture is a compressed slit and the tube is internal only. In part then the trends towards chamber reduction and development of uniserial chambers in both buliminids and nodosariids may also relate to parasitic feeding strategies.

Highly compressed biserial genera like *Bolivina* and *Textularia* which are very unstable hydrodynamically (figure 4.7), and the more stable triserial, *Bulimina*, also occur on firm substrates and Haward (1977) has shown how *T. truncata* apparently orientates its rudder-shaped test parallel to the currents when living between the ornamental ridges of a bivalve shell. Hydrodynamically unstable, elongate, forms (blades) are therefore not necessarily restricted to quiet habitats and an infaunal strategy.

Low trochoid genera, which Lipps supposes adapted to an active or temporarily fixed life as herbivores, are the most abundant group and make up 20 per cent of all genera, largely because of the dominance of this coiling mode among the rotaliids (52 per cent). To this total can be added the hemispherical, fixed, agglutinating forms (some 2 per cent of the whole) which have the same, hydrodynamically stable, limpet shape ideally suited to life on the shallow shelf and attachment to various substrates. The percentage of low trochoid genera is even higher among the planktonic rotaliids, but here the test tends to become globular with strong trends towards the perfect sphericity (attained in *Orbulina*) appropriate to a floating life. Significantly, 20 per cent of the planktonic rotaliids are planispiral, often with extended chambers. This lateral flattening appears to be an adaptation which lowers the sinking rate, as do the long, flexible spines present in many of the planktonic genera until reproduction. The spines also help to spread the net of pseudopods.

Among the Larger Foraminifera the most common coiling modes are planispiral fusiform, almost 50 per cent of the Fusulinida and 10 per cent of the Miliolida, flattened planispiral, annular discoidal, particularly well developed in the lituolids (8 per cent) and in the miliolids (7 per cent) and annular complex, 8 per cent of the rotaliids. As noted above the frequency of the individuals of the species among the Larger Foraminifera and thus the success of the life strategies these modes represent is much greater than those figures seem to suggest. Recent Larger Foraminifera appear to be confined to shallow shelf environments in the tropics and the extinct fusulines and orbitoids probably occupied similar habitats. Bandy (1960a) notes how simple discoid genera occupy extremely shallow depths, 0 – 30 m, while discoid forms with chamberlets, fusiform genera and annular complex genera occupy the 20 – 80 m depth range. It seems clear that these modes and the characteristic external shapes can again be related to hydrodynamic factors and in particular to the exigencies of a symbiotic life in association with algae (Haynes, 1965; Ross, 1974).

It was pointed out by Smout (1954) that the shapes in Larger Foraminifera tend to those that give maximum surface to volume ratio. He also noted that the effect of the main morphological trends in the larger rotaliids, involving the introduction of chamberlets as well as annular and cyclical growth, is to reduce the tendency for the successive lamellae to build up into a thick mass. Thus in *Nummulites*, although the successive 'instars' build up a massive marginal cord, the lamellae thin out on the side walls with the introduction of meandrine filaments. In annular complex genera such as *Miogypsina* the lamellae become buckled to form the lateral chamberlets.

Figure 4.7 shows the major types of Larger Foraminifera grouped according to Zingg's classification of pebble shapes. Maximum sphericity and perfect adaptation to current swept reefal conditions is seen in *Gypsina* and *Baculogypsina* which also possesses strong spines to assist lodgement. In these genera, as in *Orbulina* which is equally well adapted to a planktonic life, the ratio of surface to volume is low. As noticed by Smout, the majority of Larger Foraminifera show much lower sphericities and it is very striking how they are found to fall mainly between the 0.5 and 0.7 lines of intercept sphericity with discs, flattened spheres and rollers. Although very different to the eye these shapes are of equal hydrodynamic stability. Thus disc-shaped *Marginopora* and roller-shaped alveolines would have equal stability in the same environment. The miliolids are largely epiphytic and the discoid shape allows firm attachment to algal fronds and sea grasses as well as to sedimentary substrates. The milioline coiling of many of the smaller genera such as *Quinqueloculina* also produces a globular to fusiform shape which together with the very smooth surface allows the foraminifer to move freely in weed with least danger of being swept away by currents.

The apparent tendency for Larger Foraminifera to sacrifice hydrodynamic stability to achieve a greater surface to volume ratio as well as keeping the outer walls thin is probably connected with the storage of symbiotic algae which depend upon adequate light penetration. These are known in the annular discoid genera *Marginopora* and *Cycloclypeus* as well as in the fusiform *Alveolinella*. Ross (1972c) has recorded how the algal symbionts in *Marginopora* which attaches itself to the substrate by the pseudopods migrate to the well-lit side, and he has also observed (Ross, 1974) that the outer walls remain highly transparent during life. Flattening to achieve a maximum surface to volume ratio is also seen in *Heterostegina* which, as already discussed in chapter 3, can subsist entirely by symbiosis, living attached within a hyaline sheath (Röttger, 1972). It seems logical to assume that the extinct allies of *Heterostegina* and *Cycloclypeus* within the Nummulitidae, in particular *Nummulites* (planispiral lenticular to globular) and *Spiroclypeus* (subannular complex), followed similar life strategies and that the very large species of *Nummulites* were also sessile. Complex canal systems are found in this group and are probably connected with the metabolic requirements of this type of nutrition. (See further in chapter 13.)

Increased stability and strength without changing the shape is achieved in these genera by adding to the mass. This explains the remarkable tendency of the large rotaliids and orbitoids to deposit secondary calcite in the form of pillars at the corners of the lateral chambers and within the septa, or as umbilical bosses, while keeping the outer walls thin.

The roller-shaped fusulines and alveolines show similar trends. Dunbar (1963) finds that the largest schwagerinids show the 'surprising' tendency to both thinning of the outer wall by honeycombing and to deposition of axial deposits. Similar internal deposition of secondary calcite (flosculinisation) takes place in the alveolines while, again, the outer walls remain thin.

The Adaptive Significance of Wall Structure

Agglutinated tests of adventitious material appear to have been the first hard shells to appear in Foraminifera, and the adaptive success of this type of wall structure is shown by the abundance of the agglutinating group at all depths. Significantly, non-calcareous members of this group dominate in extreme environments, as on the abyssal plain below the CCD, in silled basins and in marginal marine conditions of lowered oxygen and salinity. Most genera in marginal marine and shallow water environments are simple, whereas forms with complex interiors, such as *Cyclammina*, are more common in deeper water (Bandy, 1960a).

In 'normal' marine environments a secreted calcareous test frees the foraminifer from dependence on bottom material and allows the construction of a lighter, architecturally more complex shell. The evolution of this type of wall was clearly a factor in the development of floating brood chambers and the invasion of the pelagic realm by the planktonic families. The appearance of lamellar structure was also a considerable evolutionary step, as it allowed adaptive radiation along a number of different lines and, in particular, the development of annular complex structure. It also allowed the development of spines, costae and keels by localised thickening which are such a feature of the planktonic families and also of benthonic groups like the buliminids, especially in deep water on soft substrates.

The occurrence of several, sharply different, types of calcareous wall structure, characteristic of different major groups, strongly suggests adaptive radiation. It is possible that this variation, like the trend towards a test shape with a high surface to volume ratio and thin outer wall, also relates in part to a symbiotic feeding strategy. This is because the dependence of algae (or sequestered chloroplasts) upon adequate light means that symbiotic Foraminifera are restricted to the photic zone.

The maximum depth of the photic zone is taken to be where green plus blue light is reduced to 1 per cent. This appears to be at about 120 m depth in the very transparent centres of the ocean gyres in the tropics, such as the Sargasso Sea (Steemann-Nielson, 1975). The water is always less transparent at higher latitudes and in coastal areas with corresponding restriction of the photic zone.

The compensation point, where respiration begins to exceed photosynthesis in diatoms, is at about 50 m in the English Channel on a sunny day in midsummer (Harvey, 1963) when the light energy equals that in the tropics. Photosynthesis is at a maximum between about 15 m and 5 m and falls off markedly from 5 m to the surface due to the inhibiting effect of ultraviolet light. In very bright light it is arrested due to contraction of the chloroplasts. Effective symbiosis can therefore only take place in a narrow range of water depths. In these circumstances it would seem likely that any advantage that might accrue from wall structure, especially the appearance of semi-translucent or glassy shells, would be of great adaptive significance. Also, it may be that different wall structures allow symbiotic genera to exploit different depths within the phototropic zone.

In the simple, agglutinated *Iridia* the algae are carried outside when the pseudopodia are active (Cushman, 1922). This process, which apparently ensures effective photosynthesis, has also been observed in the planktonic Foraminifera (Hemleben *et al.*, 1977; Bé *et al.*, 1977). However, it seems very probable that a wall structure that allows the algae to photosynthesise within the test, as appears to be the case in the Larger Foraminifera in particular, confers a positive advantage. The hyaline wall, especially radial structure, possibly has an adaptive advantage towards the deep limit of the phototropic zone and it is significant that the large rotaliids and the planktonic Foraminifera are all radial. Again, although at the present day the major types of hyaline wall occur at all depths, it is also significant that families with oblique structure such as the Cassidulinidae, Chilostomellidae, Nonionidae and Pleurostomellidae are a particular feature of cool, deep water. In contrast, the porcelaneous group are particularly abundant in shallow waters, especially in the tropics on the inner shelf in open bays and lagoons (Bandy, 1960a; Murray, 1973b). This distribution suggests that porcelaneous structure may bestow a protective advantage, the crystal arrangement helping to scatter short wavelength, ultraviolet light. The fact that *Marginopora* has been found to have clear windows in the outer chamberlets where the symbionts are concentrated, created by the alignment of the calcite laths perpendicular to the surface (Ross and Ross, 1978), can be taken as evidence of an exception that proves the rule. The thick brown organic membranes characteristic of miliolids and peneroplids may also absorb the short metagenic wavelengths. Agglutinated structure may also be an advantage at these shallow, extremely well-lit depths, the layer of grains embedded in the organic membrane performing the same protective function. This may explain the success of the large, fusiform, arenaceous genus *Loftusia* during the Maastrichtian stage. Similar considerations may help to explain the variations in the number and thickness of the layers in the microgranular fusulinids.

It must be emphasized to the student that these ideas on form and function are largely speculative and require much more research on living Foraminifera for their confirmation or rejection. As Morley Davies (1939) said in another context:

> Here I must end. I have shown you some of the problems and puzzles that confront palaeontologists as soon as they attempt something more than empirical treatment of the fossils they collect. Such feeble attempts as I have made at explanations are only gropings in the dark; but I hope some of you who are concerned with living molluscs may be able to throw some light on the secrets of the dead. Even if you can only show that my own suggestions are absurd and impossible, that will be better than nothing.

SUMMARY

The Foraminifera present a unique variety of test shapes and coiling modes. The majority are multilocular and characteristically the test has a restricted aperture and internal foramina and a toothplate is often present. The main kinds in order of abundance (total genera) are low trochospiral, high trochospiral/uniserial, planispiral lenticular, fusiform, biserial/uniserial, discoid, milioline, uniserial, polymorphine and annular complex. Mixed growth is common and it has been assumed that ontogeny reflects phylogeny with the stages shown most completely in the B form. This is supported by the stratigraphical evidence.

The test wall which is either of agglutinated grains or of secreted calcite is built up on a tectin membrane. The agglutinated grains may be carefully selected for size, shape and composition and are bound with organic cement. This is usually ferruginous, and under normal marine conditions, often highly calcareous. In the calcareous Foraminifera the wall is either microgranular (fusulines) or composed of randomly arranged calcite laths (porcelaneous—miliolids) or of rhomboid microcrystals (hyaline group) showing the complete range of orientations possible for calcite—on the a-axis, on the c-axis and on the rhomb face. Compound structures and tests composed of a single crystal also occur.

Hyaline Foraminifera are generally lamellar: either monolamellar, where each chamber is composed of one layer which invests the previously formed test, or multilamellar. In this latter group the wall is usually bilamellar, with two layers of calcite on either side of an organic membrane. The inner calcite lamella may coat the previous apertural face as a ‘septal flap’.

The walls of hyaline Foraminifera are perforated and pores also occur in many genera of the microgranular and the agglutinating groups.

Growth of a new chamber in the hyaline group involves the active participation of the pseudopods and begins with the formation of the tectin membrane and by the secretion of calcite in patches which gradually coalesce to form the wall-like pieces of a jig-saw puzzle. The units are first granules but later become euhedral. In the porcelaneous group the process is rather different and involves the gradual mineralisation of a thick organic ‘moulage’.

Two views prevail regarding the sequence of events in the formation of the bilamellar wall which is believed either to be built up step by step on the basis of the tectinous or ‘chitinoid’ inner lining or to result from simultaneous secretion of inner and outer calcite lamellae on either side of the organic ‘median layer’. In the first case the wall is considered to be built around the organic tubules which become the pore linings; in the second the pores are considered to arise later by resorption.

As well as providing a foundation for the construction of the hard shell the organic membranes act as a shield against physical and chemical changes. The organic pore plugs are minutely perforated and probably act as a fine filter. When necessary, the aperture and foramina as well as the pores can be completely closed off.

The hard test may have arisen to control buoyancy as well as being a protective device and the multichambered form affords extra protection against external physical and chemical effects and extends the time available for osmoregulatory adjustment.

The different coiling modes appear to relate to feeding strategies as well as to environmental, especially hydrodynamic, effects. Their repeated appearance in the different wall structure groups indicates adaptive convergence, with low trochoid forms occurring mainly as active herbivores in shallow water, high trochospiral/uniserial forms as deposit feeders at the sediment/water interface and infaunally and planispiral genera as active deposit feeders in weed and on soft substrates. The Larger Foraminifera occur in weed and are attached by their pseudopods to the sedimentary substrate in shallow water in the high energy zone, and their disc and roller shapes appear to represent a compromise between the requirements of a symbiotic life involving a high surface to volume ratio and hydrodynamic stability. Simple correlations between morphology and habit are not possible because a particular coiling mode may allow more than one feeding strategy and many genera are opportunistic, omnivorous feeders. The occurrence of mixed growth may indicate changing requirements during ontogeny.

The plastic response of Foraminifera to environmental pressures, together with convergent evolution in the major groups which often appears to have 'followed curiously devious paths', makes it difficult to assess the adaptive significance of wall structure. In general, the agglutinating group dominates below the CCD and in marginal marine environments, while the calcareous groups dominate 'normal marine environments'. The appearance of the calcareous wall and, in particular, lamellar bonding has allowed the construction of lighter, stronger tests and led to adaptive radiation along a number of different lines, including the rise of annular complex genera and forms with complex canal systems. Foraminifera are unique in exploiting all the preferred orientations of calcite as well as producing a random array of calcite laths. This may in part relate to the symbiotic feeding strategy which is restricted to a narrow range of depths in the phototropic zone. Radial structure may have an advantage towards the deep limit, 50 m plus, while porcelaneous structure may have a protective advantage at very shallow depths near the surface.

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Chapter 5

Classification of the Foraminifera

> The extent to which progress in ecology depends upon accurate identification, and upon the existence of a sound systematic groundwork for all groups of animals, cannot be too much impressed upon the beginner in ecology. This is the essential basis of the whole thing; without it the ecologist is helpless, and the whole of his work may be rendered useless.
>
> (Elton, 1966)*

Scrupulous taxonomic work is fundamental to the use of Foraminifera in both stratigraphical and ecological studies. This is because precise zonal stratigraphy and palaeo-ecological reconstruction depend upon precise discrimination of species. Species are defined as natural, interbreeding populations, with a distinctive range of form, reproductively isolated from one another and occupying a definite ecological niche. New species become established in response to selection pressures at work on genetically variable populations with adaptation of favoured variant populations (subspecies) to suitable, new ecological niches. With time and geographical isolation, the subspecies of such 'polytypic' species develop into new species (allopatric speciation). New species may also arise by gradual change of a population through time, caused by the spread of beneficial mutations which either confer a competitive advantage or allow adaptation to changing conditions (sympatric speciation).

Closely related species, when viewed at any one time, as we see living species at the present day, may appear to be separated by morphological gaps. We see them frozen as in a snapshot. But traced through space and time we find that both allopatric and sympatric species are linked to their ancestors by intermediate forms in a morphological gradient (cline). As Glaessner (1945; see reprint 1963a) said: 'with increasing knowledge ... of successive populations, boundaries between successive species become more indefinite.' It may therefore be necessary to set arbitrary limits between closely related subspecies and species. This is not quite such a problem in palaeontological practice as might be feared, because of the, apparent, general prevalence of allopatric speciation. New species develop from subspecies at the periphery of a species range. When conditions change the ancestral form may die out and be replaced by one of its descendants which is then able to migrate into the old homeland. In a vertical geological section the new species will appear to replace its ancestor without passing through an intermediate phase. Again, it may appear abruptly in a new area apparently without antecedents. As the geological sequence is inherently episodic the ranges of most foraminiferal species are of this type. This is convenient for correlation on the basis of empirical index fossils (species where the known range only approximates the life range) but creates difficulties in tracing phylogeny. It follows as a corollary from these considerations that although the presence of a distinct gap may aid in definition of allopatric species the converse, the presence of intermediates, cannot necessarily be taken as a justification for 'lumping' them under one taxonomic head. It must also be kept in mind that species and subspecies from different environments occur mixed together in foraminiferal death assemblages.

Species of Foraminifera are distinguished largely on the basis of chamber shape and number and also by the type of ornament where this is present. The fine structure of the wall may also differ at the specific level. Minor variations in these features may distinguish subspecies but it must be pointed out that all local populations will differ from each other in some degree. Species which, because of their general similarity, are deemed to be of common descent are grouped in genera. This is the basis of the binomial nomenclatural system of Linnaeus (1758) whereby each species has a first (generic) name and a second (specific or trivial) name. A third, infraspecific name (trinomial) is added in the case of subspecies.

**Animal Ecology* (first publ. 1927). Sidgwick & Jackson, London.

Genera of Foraminifera are distinguished as far as possible on the basis of qualitative differences in chamber arrangement, aperture position and tooth structure but again gradations inevitably exist. The presence of a keel is considered diagnostic at the generic level in some groups, *Globorotalia*, but is a specific feature in others, *Elphidium*. The same applies to certain details of wall structure. This underlines the importance of taking all the features of the test into account in classification.

A major problem in palaeontology is that identification has to be made on the basis of an incomplete fossil sample, and the range of form and limits of the breeding population are a matter of inference. In the case of Foraminifera, dimorphism and age differences, particularly of multiform species, must also be taken into account, i.e. the species may be composed of several homogeneous groups or 'phena' (sing. phenon). Genetic variation in structure, chamber shape and number, and ornament must be distinguished from variation related to environmental influences. Difficulties arise because overall size, as well as thickness of the wall and strength of ornament, may vary with changes in salinity and temperature. It is also necessary, in view of the importance of the last chambers in classification, to recognise retardation or stunted growth (kummerforms). Abnormal growth may follow injury or attack by predators and attached species commonly show great irregularity of form.

The difficulties caused by the effects of fossilisation must also be faced. This becomes particularly acute in the case of Palaeozoic species, where the layering in the walls may be destroyed by recrystallisation and dolomitisation or silicification. Certain agglutinated species are particularly prone to collapse and distortion. Aragonitic species are subject to rapid solution and may be represented only by internal casts. Even in the Tertiary, alteration may be severe. At some levels of the Paleocene in the Libyan Sahara, Foraminifera are entirely made over into casts of dolomite crystals, some of which, however, can be identified by careful comparison with the unaltered fauna at other levels (Haynes, 1962). On the other hand, Foraminifera may sometimes survive even in metamorphic terrains, and Raguin (1925) has reported a case from the Vanoise Mts. of the Alps where specimens of *Globotruncana* are preserved in albite phenocrysts!

In cases where an identification of a species is uncertain because of paucity of material or preservation, a question mark is placed after, or the abbreviation cf. ('similar to') is placed before, the trivial name. In cases where the material clearly shows an affinity to a known species but the precise relationship is uncertain the abbreviation aff. is used. Where the material appears to represent an infra-specific category but its status is uncertain it is often found convenient to use the term 'form'. The term 'group' (*ex gr.* = of the group) may be used for a number of species apparently related but of uncertain affinity, i.e. *Lenticulina ex. gr. muensteri*. Groups of species of this kind are regarded as superspecies if they can definitely be shown to comprise several, closely related, sibling species. Species commonly comprise several subspecies and again in cases of uncertainty it may be necessary to refer material to a subspecies group, with *subsp. gr.* or simply gr. placed after the trivial name.

In this connection it is useful to look at some examples of 'difficult' species. These illustrate very well some of the problems of recognising species and subspecies represented by variable populations and the application of informal nomenclature (plate 8). Quaternary groups have been chosen as they have the advantage of ranging into the Recent.

The first example is the variable group of species that includes *Elphidium excavatum*. This can be regarded as a superspecies, including *E. clavatum* and *E. selseyense* and their allies as siblings of *E. ex gr. excavatum*. On the other hand, this group can be regarded as one polytypic species, the *E. excavatum subsp. gr.* (plate 8).

Elphidium is a planispiral, involute genus distinguished by a lamellar and perforate calcareous wall and pits along the sutures, separated by septal bars and often joined by slits, which connect with an internal canal system.

Plate 8, nos. 8 – 13, show some of the closely related kinds of *Elphidium* that at various times have been referred to *E. excavatum*. They can be distinguished on the basis of ornament and relative development of sutural slits, sutural pits and septal bars. *Elphidium excavatum* s.s. *(sensu stricto)* is relatively compressed and smooth with only moderately developed pits and bars. *E. incertum* is also smooth but with prominent sutural slits and only weakly developed pits and bars. *E. clavatum* (originally described as a variety of *E. incertum*) is distinguished by its strong, single, umbilical bosses, while in *E. selseyense* the umbilical ornament consists of a variable cluster of small granules which also extend along the sutures. In addition, the periphery of the test is more rounded in *E. selseyense* and the test more densely perforate.

E. clavatum was originally described from the N.E. Atlantic, whereas *E. selseyense* was described from the English Channel. Subsequent collecting has shown that although intermediates exist with small granules around a larger central boss, *E. clavatum* is characteristic of high latitudes today and is often a dominant in cold water Pleistocene faunas, while *E. selseyense* is characteristic of temperate latitudes. This suggests a morphological continuum with distinctive 'end members' in different geographical areas that are conveniently regarded as separate species. However, as might be expected, Scandinavian and German workers have faced a particular problem with intermediates which has led Feyling – Hanssen (1972) to consider them both merely forms of *E. excavatum*, together with the Lusitanian and Mediterranean *E. lidoense* which has a broad umbilical development of medium-sized, round, granules (papillae), i.e. *E. excavatum* forma *lidoense*. This view is in sympathy with that of Poag (1978) who regards such species with distinctive end members distributed along an ecological gradient as 'paired ecophenotypes'.

Distinctive stratigraphical distribution and utility must be the yardstick for the recognition of subspecies and species in palaeontology where doubt will always remain about the taxonomic status of different population groups. In practice, it is difficult, if not impossible, to distinguish between subspecies and 'ecophenotypes' which in any case are potential if not actual subspecies. My own view, on consideration of the geographical ranges of *E. clavatum, E. lidoense* and *E. selseyense* and their occurrence in the Quaternary, is that they are worthy of at least subspecific distinction. There is certainly no case for sweeping all these groups together as infra-subspecific variants, without names, under one specific head, as has been suggested (Hansen and Lykke-Anderson, 1976), for this would completely obscure the stratigraphical and ecological information that is revealed by their precise recognition.

That the true relationships of *Elphidium ex gr. excavatum* are quite complicated is indicated by the fact that *E. incertum*, which apparently only differs from *E. clavatum* in lacking umbilical bosses, is sharply distinct in its hyaline-oblique wall structure from all the other members in the group, which are hyaline-radial. It is also noteworthy that *E. williamsoni*, which differs from *E. excavatum* s.s. in its rotundity and strongly developed pits and septal bars and shows a general restriction to estuarine and marsh habitats, has been found to show marked chloroplast symbiosis by Ellen Christensen (1977). In contrast, *E. selseyense (E. excavatum* in her sense) showed no evidence of chloroplast symbiosis, which fits with its wider ecologic range (euryhaline) and tendency to occur deeper in the sediment. This would seem to prove the value of distinctions made on the basis of external morphological features alone.

The question may now be asked whether breeding experiments in tanks can contribute to the solution of some of these problems. These have not been done with *Elphidium ex gr. excavatum* but have been carried out (Bradshaw, 1957, 1961; Schnitker, 1974a) with members of *Ammonia ex gr. beccarii* which presents similar taxonomic problems.

Schnitker claims that the offspring of *Ammonia tepida* raised in tanks exhibited a range of variation which included all the other six main *Ammonia* species that occur along the North American east coast. Three of these were figured. He also claimed that *A. beccarii* s.s. collected from N. Carolina also produced offspring identical with several of these forms but in this case neither the parent or offspring were figured. However, on this basis he suggests that *A. ex. gr. beccarii* is one species only and that the subgroups are infra-subspecific and should be differentiated merely as forms. Plate 8 shows some of the European members of *A. ex gr. beccarii* separated as species by various authors. On the basis of Schnitker's experiments these could all be considered variants of one species. But individuals from the population of *A. beccarii* in its type area in the Adriatic have yet to be studied in tanks, and many known variants did not appear during the course of Schnitker's study. So it seems reasonable to continue to regard *A. ex gr. beccarii* provisionally as a superspecies comprising several, closely related, polytypic species of common origin which because they, apparently, exhibit 'reticulate evolution' through the Quaternary can be considered as a plexus.

The flattened *A. limnetes* (plate 8, no. 6) appears to be distinct specifically from the large, many-chambered *A. beccarii* s.s. (no. 1). On the other hand *A. batava* (no. 2) and its unornamented form *A. aberdoveyensis* (no. 7) closely resemble the *A. sobrina* series illustrated

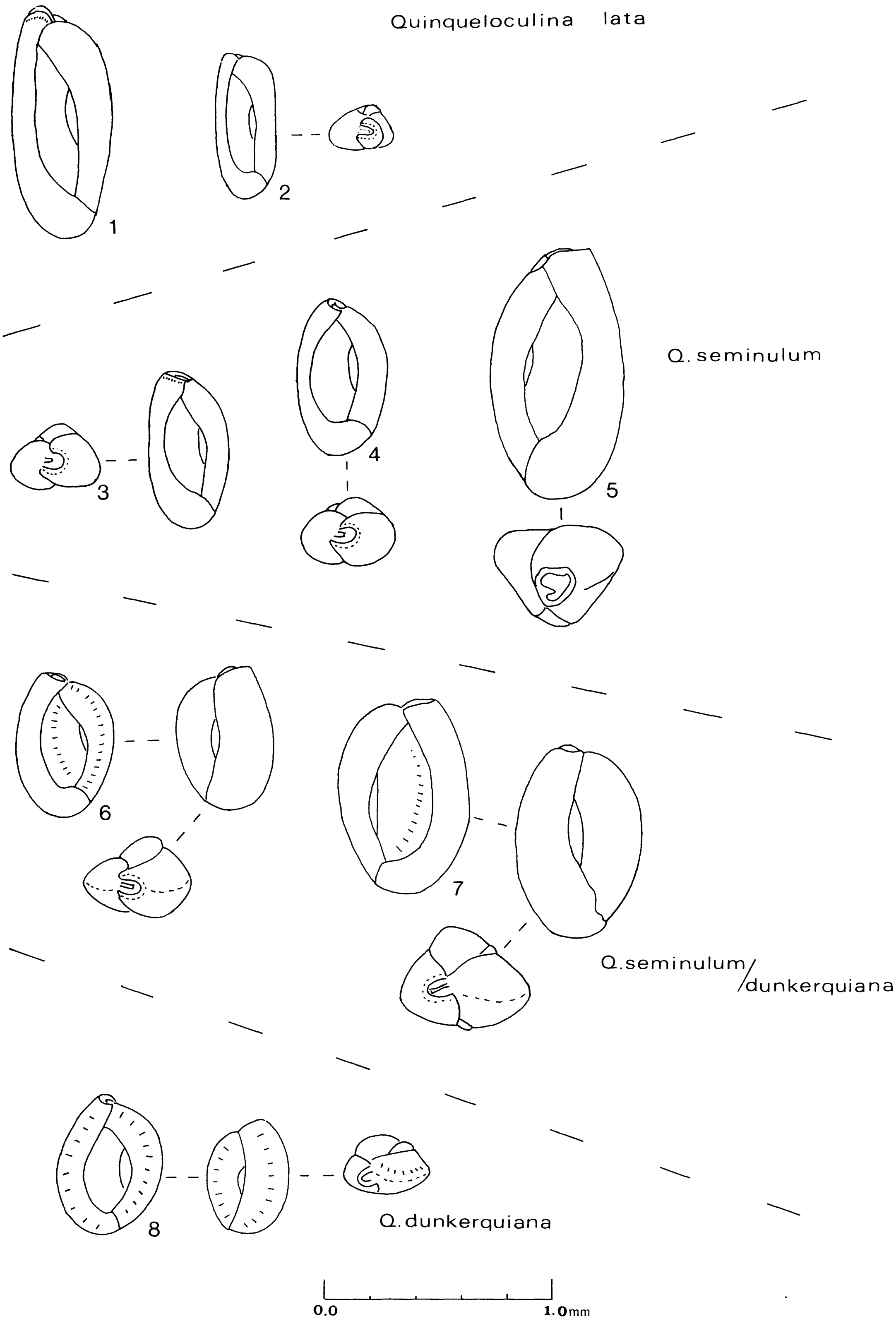

Figure 5.1 Species of the group *Quinqueloculina seminulum*

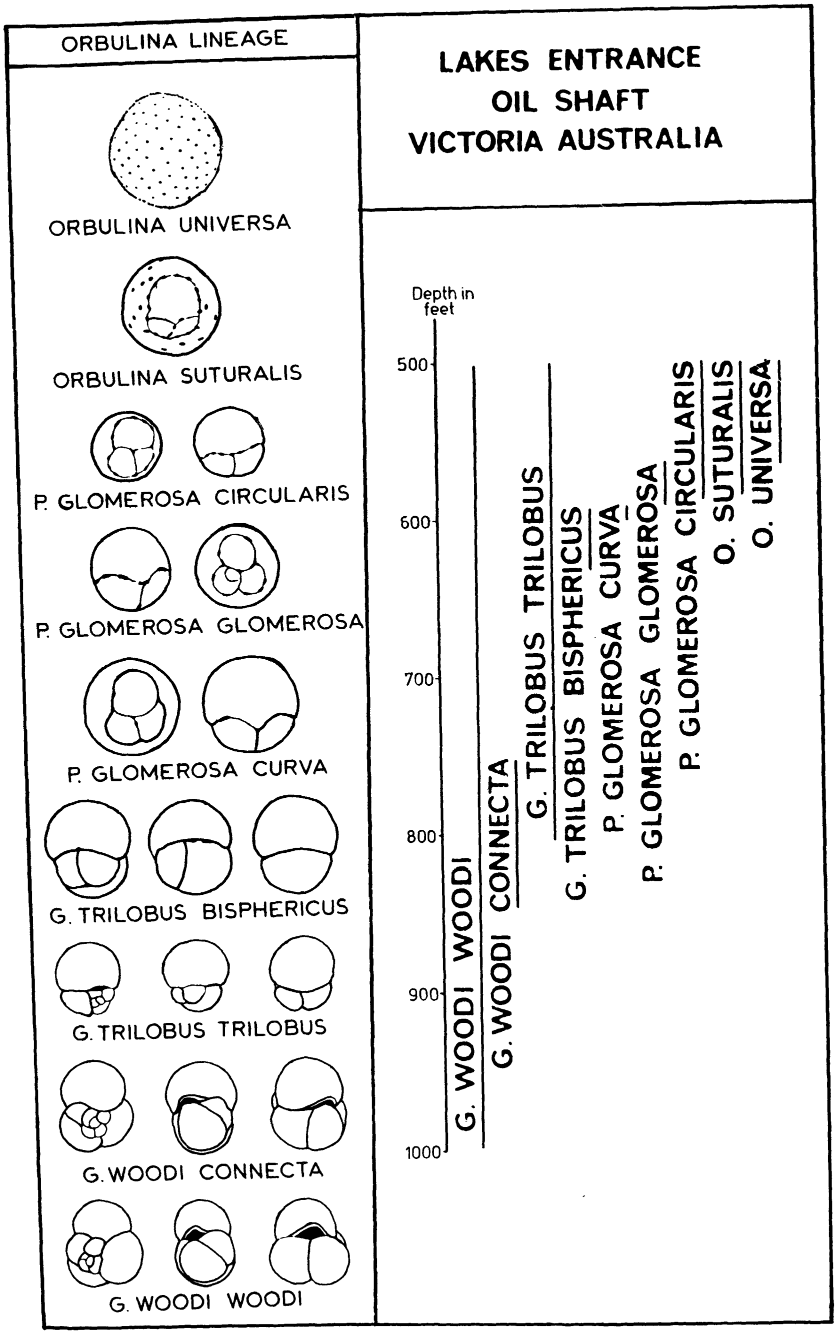

Figure 5.2 Occurrence of the *Orbulina universa* lineage in the Lakes Entrance Oil Shaft, Australia. After Jenkins (1968)

by Schnitker. *A. sobrina* differs only in its development of single, elongate bosses on the umbilical lobes rather than clusters of a few round bosses. These groups presumably represent different populations of one species on either side of the Atlantic. *A. tepida* appears to be a variant favoured by high temperatures that appears in both groups, possibly with *A. flevensis* as a low salinity form. *A. aberdoveyensis* appears to be an unornamented, low salinity form of *A. batava*. Further tank experiments and study of the response to both salinity and temperature controls with application of population statistics (Mayr, 1969) would help in definition of *A. ex gr. beccarii* and the results would assist solution of similar problems in extinct superspecies.

The same objection can be made against simply sweeping all the variants together in one species, as was made in the case of *Elphidium ex. gr. excavatum*—that their recognition is too valuable in Quaternary stratigraphy. For instance, *A. batava aberdoveyensis* is a dominant on the present Dovey marshes in West Wales, but *A. limnetes* and *A. batava tepida* dominate the Holocene marsh succession penetrated in boreholes (Haynes and Dobson, 1969; Haynes, Adams and Atkinson, 1973). Further, the informally designated *Ammonia* species A (no. 4) is characteristic of many Ipswichian (last interglacial) successions around the southern Irish Sea and in Somerset but has not yet been found living in the same area.

In cases where species can be shown to be linked in a morphological series, compound names have sometimes been used for the intermediates, as in the case of the *Quinqueloculina seminulum* group by Dupeuble *et al.* (1971). This may be useful as a provisional step before the taxonomic categories can be properly worked out. Figure 5.1 shows this method applied by Haynes (1973) in the Irish Sea, where most of the population may be defined as *Q.seminulum/dunkerquiana* but where the extreme end-members, elongate, parallel-sided *Q.lata* and short, angled *Q.dunkerquiana* also occur rarely. It is probable that this is another example of a polytypic species comprising several intergrading subspecies. It may be possible to recognise the end members as species if they are geographically and ecologically distinct but clearly the limits between the subgroups, however chosen, will be somewhat arbitrary. Ultimately, the dynamics of speciation in the group will only be understood when its history is traced through time.

A morphological series that can be traced through time to show a definite line of descent is distinguished as a lineage. Such lineages are most important in stratigraphy because the most accurate zones available for stratigraphical correlation are biozones (stratal intervals distinguished by life ranges of fossils) based on the steps of a lineage where the appearance and disappearance of species and subspecies can be pinpointed in a vertical section (the rational index fossils of Glaessner, 1966). A good example of such a stratigraphically useful lineage is that which includes *Orbulina universa*. This has been worked out in detail by Jenkins (1968) in the Lower Miocene of the Lakes Entrance Oil Shaft, Victoria, Australia (figure 5.2). The lineage includes nine taxa, commencing with the central type of the polytypic *Globigerina woodi* distinguished by its single, arched, umbilical aperture.

The line of descent is as follows:

Globigerina (single umbilical aperture)	*woodi woodi* (arched aperture) *woodi connecta* (low aperture and greater size increase of chambers as added
Globigerinoides (extra dorsal apertures)	*trilobus trilobus* (reduced umbilical aperture, enlarged last chamber) *trilobus bisphericus* (last two chambers make up most of the test)
Praeorbulina (globular last chamber, sutural apertures only)	*P. glomerosa curva* (one or two apertures per chamber of the *Globigerinoides* stage) *P. glomerosa glomerosa* (three or four apertures per chamber) *P. glomerosa circularis* (numerous apertures)
Orbulina (areal apertures)	*O. suturalis* (sutural apertures define *Globigerinoides* stage) *O. universa* (unilocular)

As can be seen, the subspecies and species are linked by gradational changes in chamber and aperture shape and number, while the genera are defined by qualitative changes in aperture position. There is a gradual reduction in chamber number until the single-chambered stage of *Orbulina universa* is reached. Jenkins suggests that the spherical test may have a buoyancy advantage in the planktonic environment.

Jenkins has also been able to recognise the lineage in Lower Miocene sections in New Zealand. This suggests that the same stages were reached at approximately the same time in the S. Pacific and can be taken to define accurate biozones. From radiometric data the lineage is considered to have spanned some 8 million years, the first 2 taxa appeared in 6 million years, the last 6 taxa in only 2 million years. Of particular stratigraphical importance is the time of appearance of the final stage, *Orbulina universa*, near the L. Miocene/M. Miocene boundary. The first appearance of this striking form has been taken as a worldwide datum but it appears to occur earlier, below the boundary, in the tropics and progressively higher in the Middle Miocene in high latitudes (Bandy, 1966). Thus, although the appearance of the final stages of the lineage can be considered geologically instantaneous in the tropics, it took some millions of years for *Orbulina* to spread into the northern and southern oceans. This was no doubt connected with climatic and other geographical factors. It shows that the most carefully defined biozones, even when based on the life ranges of cosmopolitan planktonic species, are likely to transgress time lines outside the region of definition.

The *Orbulina* lineage might be taken as an example of sympatric speciation with gradual shift of the mode with time, but the persistence of some of the species indicates that it probably is a case of allopatric speciation with adaptation of different subspecies to different depth zones of the water column. Inevitably, they occur together in the death assemblage on the sea bed.

FORMAL DESCRIPTION OF SPECIES AND THE RULES OF NOMENCLATURE

Precise discrimination of species requires their precise definition by means of a full *description*, with accompanying figures and exact naming according to the International Code for Zoological Nomenclature (ICZN) 1964. Under the Linnean binomial system the specific name is based on a single specimen, the *holotype*, selected to represent the combination of characters that distinguishes the species. These distinguishing features are listed in a *diagnosis* that accompanies the description. According to the *Principle of Priority*, established by the International Code, a name that has been used previously for another species within the genus must be rejected as a *homonym*—the same name for two different taxa. If the species has already been given a name, the later (junior) name must be rejected as a synonym—a different name for the same taxon. This rule is subject to certain qualifications. The prior name must be valid in that it has been published according to the International Code in a scientific journal or book, accompanied by a description and/or figure that makes identification possible. Also, it must follow the Linnean binomial system which rules out names applied before 1758 and the 10th edition of the *Systema Naturae* (Linnaeus, 1758).

The same rules apply for generic names as for specific names and in this case if the same name has already been applied to another member of the Animal Kingdom it must be rejected as a homonym. The genus is founded on a selected species so the holotype of that species also becomes the *genoholotype*. Again, if a previous author has already made that species the type of a genus, then that name takes priority as a *senior synonym*.

Such is the importance of type specimens, described by Owen (1964) as, 'the greatest treasures of Natural History Museums', that a number of recommendations are made under the International Code for their safe-keeping. These include their deposition in a museum or other institution where they will be safely preserved and made available for purposes of research and be given unmistakable labelling to indicate their status, the details to be published.

The International Code recognises four categories of *primary types* apart from the holotype. When the original author has selected his holotype from a *type series*, the remaining specimens are regarded as *paratypes*. If, as in the case of some older species, the author has not designated one as the holotype, then all the specimens of the type series are regarded as *syntypes* of equal value in nomenclature. When the holotype has been lost or one was never selected, it is open to a subsequent worker to designate one of the syntypes or paratypes as a *lectotype*. In the event of the proven loss or destruction of all the original type material, a subsequent worker may erect a *neotype* on the basis of a specimen from the same locality and horizon as the original type. This must be done with great care and with regard to other well-established species in the genus, in order that it achieves the aim of contributing to the stability of nomenclature rather than disturbing it. Deposition of a neotype in a museum or other institution is mandatory.

A number of secondary type terms have been proposed in addition to these five primary types recognised by the ICZN. Simpson (1940) collected over 80 such terms, including 'museotype' for a specimen in a museum! Undoubtedly, most of these are confusing and best ignored, apart from *topotype*, applied to a specimen that comes from the same locality and geological zone as the holotype or syntypes of the species. Such specimens will have the best chance of being from the same population as the holotype and in the case of its loss will best serve as neotypes.

Description

A full formal descriptive treatment of a new species includes the following items:

Scientific name and author
Synonymy (if required).
Diagnosis.
Description and measurements of holotype.

Material available for study.
Variation in the population sampled.
Provenance of type and its depository (museum number).
Remarks to supplement diagnosis and description.
Geographical and stratigraphical range.
Habitat and ecology.

The purpose of the full description is to give a rounded account of the species that will, together with the figures, enable future workers to identify it without recourse to actual examination of the holotype. It therefore goes considerably beyond the diagnosis, which is restricted to features which distinguish the species from closely related ones. The arrangement is standardised and proceeds from the general to the particular as this makes it easier to compare two descriptions point by point, especially if a concise, abbreviated style is adopted.

In the description of a species, treatment of stable generic characters is unnecessary and similarly repetition of features that apply to the species as a whole should be avoided in the description of subspecies. On the other hand, very detailed description will be necessary in poorly known groups so that characters are dealt with that may distinguish the species from others still to be described.

The description is normally restricted to the holotype, and variation in the population as a whole is dealt with separately. This has the advantage that the description can stand unaltered for the holotype if later workers split the material into a number of subspecies or species.

The features of the foraminiferal test of importance in classification at the generic and specific level are usually dealt with in this order: preservation, habit and general appearance first, followed by details of the chamber arrangement, sutures, wall structure, perforation, aperture, internal structures and external ornament. (See Summary at the end of the chapter for all the points that should be considered.)

Even the best verbal description requires illustrations and in most cases these convey more than can be expressed in words. This is accepted by the International Code which recognises names published prior to 1931 without description as valid if accompanied by a figure. With the development of the SEM there have been suggestions that we could move back to this approach in micropalaeontology, but there is no doubt that even the best photomicrographs of Foraminifera require verbal explanation. When illustrating a new species, care should be taken that the diagnostic characters are revealed. (See chapter 2 for a discussion of methods.)

Subsequent references to the species in stratigraphic work may simply involve a listing of the name with its author, but in any work which involves discussion of taxonomic matters and in the case of less well-known species, where the range is not fully established, it is normal to include it in a taxonomic appendix. The appendix will include a *synonymy* which brings together the original reference and later references by other authors with remarks about the worker's own material. The purpose of the synonymy is not only to give the synonyms but to reveal the history of changes in the generic name of the species and to bring together the references that establish its geographical and stratigraphical range as far as is known.

It will be appreciated that long-established species will have many references. Revision of these species with full synonymy is usually restricted to monographs (works covering the complete systematics of a particular group) and catalogues. Where this has been done, subsequent workers can limit their synonymies to the first reference and to the latest revision. Revision and redescription is necessary if the original description is poor or incomplete and later work confused. Discovery of new, closely related species may also make modification of the diagnosis necessary.

An example of the redescription of a species that had been much confused in the literature is that of the biserial textulariid, *Spiroplectammina wrightii*, taken from the monograph on Cardigan Bay Foraminifera (Haynes, Adams and Atkinson, 1973). It is given here in full to show how a full, formal description is arranged and some of the conventions followed in building up a synonymy.

Spiroplectammina wrightii (Silvestri)

(Pl. 3, figs 1, 2)

Spiroplecta sagittula Wright, 1891 : 417; 1902a : 211, pl 3, figs 5 – 8 (not *Textularia sagittula* Defrance).

Spiroplecta wrightii Silvestri, 1903 : 59, text-figs 1 – 6; Heron-Allen & Earland, 1916b : 42, pl. 6, figs 7 – 10; Cushman, 1922 : 5, pl. 4, figs 5 – 8.

Spiroplectammina wrightii (Silvestri) Cushman, 1949 : 6, pl. 1, figs 2 – 4.

Textularia sagittula Brady, 1884 : 361, pl. 42, figs 17, 18; Balkwill & Wright, 1885 : 332, pl. 13, figs 15 – 17; Lacroix, 1929 : 1, text-figs 1 – 12; Heron-Allen & Earland, 1930 : 72;

Höglund, 1947 : 167, pl. 12, figs 3, 4; text-figs 143–146; Colom, 1952 : 18, pl. 5, figs 41, 42; Feyling-Hanssen, 1964 : 238, pl. 3, figs 4, 5; Nørvang, 1966 : 11, pl. 1, figs 9–23; pl. 2, fig. 12 (not Defrance).

Textularia cuneiformis Williamson, 1858 : 75, pl. 6, figs 158, 159 (not d'Orbigny).

Textularia sagittula Defrance var. *cuneiformis* Goës, 1894 : 36, pl.7, figs 288–290 (not d'Orbigny).

Textularia williamsoni Goës, 1894 : 36, pl. 7, 285–287 *(nomen oblitum).*

DIAGNOSIS. A compressed, carinate species of *Spiroplectammina* reaching about 1 mm in size with up to 14 pairs of chambers in the microspheric generation which is sagittate with angle of taper about 45° and with up to 12 pairs in the megalospheric generation which has a large initial coil and tends to become parallel sided.

DESCRIPTION. (Pl. 3, figs 1, 2.) Test compressed with rounded initial part and slight waist before the commencement of the parallel sided adult part, periphery lobate, carinate; initial part planispiral followed by seven pairs of chambers, the first three increasing fairly rapidly in size as added, the last four only gradually, twice as wide as high, sutures distinct, slightly impressed, almost horizontal; wall of angular silt grains set in a tectin lining, including shell material, up to 40 microns diameter, in a finer matrix, smoothly cemented; minute oval to quadrangular openings between the grains about 1 micron in size which may be pores; aperture a low slit at the basal margin of the last chamber in the median line.

DIMENSIONS. Length 0.65 mm, width 0.36 mm, thickness about 0.15 mm. Overall angle of taper about 35°.

MATERIAL. More than 25 specimens but many damaged, particularly at the initial end in the microspheric generation and in specimens with smaller megalospheres.

VARIATION. Specimens up to 1 mm length occur and apart from the tendency for specimens with large megalospheres to become parallel sided many show waisting at different points during growth with sudden expansion in breadth thereafter. This occurs in both generations. Because of the broken nature of the material it is impossible to emulate the exhaustive investigation of dimorphism carried out by Lacroix and Höglund, but it can be said that the microspheric generation occurs rarely, microsphere about 20 microns diameter, the megalospheric generation much more abundantly, megalosphere between 50 and 80 microns diameter in 10 specimens measured with up to 12 pairs of chambers. An initial planispire of four to five chambers occurs in both generations.

DEPOSITORY. B.M.(N.H.) Slide 1970 : II : 26 : 32. Stub 1970 : II : 26 : 722.

PROVENANCE. Described specimen, Brit. Mus. Core 13.

REMARKS. This species has been persistently confused with *T. sagittula* Defrance although the type figures of that species show a large inflated form, biserial throughout and about 3 mm long. The Defrance collection was apparently destroyed in the attack on Caen during the war (1944) according to Nørvang (1966) but specimens which may reasonably be regarded as topotypes have been collected from the Pliocene of Sienna by Loeblich & Tappan (1964a). They are much larger and more inflated than *S. wrightii* and lack the planispiral initial part.

A prime cause of the confusion that has long reigned was the fact that Defrance cited the Mediterranean as an additional locality for his species which led Lacroix to suppose that *S. wrightii* was synonymous with it. There is now no doubt that Lacroix actually was working with *S. wrightii.* This also means that the attempt by Nørvang to set up a specimen of *'T. sagittula'* = *S. wrightii,* from the Bay of Villefranche as neotype for Defrance's species is unnecessary as well as offending against the Rules of Nomenclature. According to the Rules neotypes must be based on material from the type area and as noted by Loeblich and Tappan, *T. sagittula* was originally described as a fossil from Italy which indicates the Pliocene, Sienna or Castel Arquato, localities of Defrance. A further consequence is that Nørvang's attempted redefinition of *Textularia* on the basis of its 'calcitic' wall is found to be based not on the genotype but on *S.*

wrightii. This would suggest that a new generic name is required for 'calcitic' as against arenaceous species of *Spiroplectammina*. However, we believe these differences to be of specific rather than generic significance, especially as *S. earlandi,* accepted by Nørvang in *Spiroplectammina* s.s. has according to our observations calcareous grains in its wall and his own thin section of *T. sagittula* (pl. 2, fig. 12) = *S. wrightii,* includes 'insignificant amounts of quartz grains'. Both may have pores.

Textularia williamsoni Goës is apparently a senior synonym of *S. wrightii.* According to Höglund it probably represents the microspheric generation. However, he found no trace of the specimens in Goës' collection and the name must now lapse as a *nomen oblitum,* being out of use for over fifty years.

Very detailed observations have been made upon this species by Lacroix, Heron-Allen and Earland and Höglund. These indicate pronounced dimorphism with a strong tendency for two groups of megalospheric individuals, constituting the A1 and A2 generations of Hofker.

It is possible that *Spiroplectammina sagittula* of Hofker (1930) belongs here but there is doubt because he reports areal aperatures and foramina in his population.

Distribution. British records include: off Rathlin Island, Northern Ireland (Wright, 1902a), South Irish Sea (Balkwill & Wright, 1885); Western Approaches (Le Calvez & Boillot, 1967; Murray, 1970); English Channel (Heron-Allen & Earland, 1916b, 1930; Murray, 1965a); Western coasts of Britain (Williamson, 1858); Scillies (Atkinson, 1970).

Other N.W. European records include: Bay of Biscay (Caralp, Lamy & Pujos, 1970); coast of Galicia (Colom, 1952); N.E. Atlantic (Brady, 1884); Belgian coast (Cushman, 1949); Skagerak (Höglund, 1947); Holocene of Norway (Feyling-Hanssen, 1964).

Mediterranean records include: Tyrrhenian Sea (Silvestri, 1903); off southern France (Lacroix, 1929, 1932; Nørvang, 1966).

A marked Lusitanian – Mediterranean concentration appears to be indicated.

The full description is based on a specimen from Cardigan Bay considered identical with the original types. This has the advantage that if future workers decided to recognise the Cardigan Bay population as a separate, infraspecific taxon it could stand without modification.

The author of the specific name, Silvestri, is given in parentheses to indicate that the generic name has been altered since the species was first described. The synonymy is arranged according to the 'zoological system' which emphasises the sequence of names rather than strictly by date, 'palaeontological system'. This has the advantage of grouping authors that have used the same name together. Each citation includes the author's name, the date of publication and reference to the volume, plate and page numbers of the publication in which it appeared. The name of the journal or book is left out as this is more economically given in a reference list at the end of the monograph, where it can be located by author and date. It is sometimes thought desirable to give the provenance and present whereabouts of each author's specimens also. However, in this case the synonymy is restricted to synonyms and references from the N.E. Atlantic area accompanied by a description and figures, so provenance is included with other records in the 'Distribution' section.

The synonymy shows, as further amplified under 'Remarks', that *Spiroplectammina wrightii* has been confused by a large number of workers with the Pliocene species, *Textularia sagittula* Defrance, beginning with Brady in 1884. For an illustration of *T. sagittula* see key figure 6.10 (nos. 3/4).

Note that *Spiroplectammina wrightii* appears to be restricted to the Lusitanian province. It should therefore be appreciated that specimens referred to *T. sagittula* (by authors following Brady) from other parts of the world, both from the Recent and from the stratigraphical column, require further study. As their taxonomic status is uncertain and they are probably unrelated to either *S. wrightii* or *T. sagittula,* they are necessarily excluded from the synonymy.

Wright realised that specimens collected off the Irish coast were different from the species of Defrance because they possessed a large initial coil, and although he identified them as *sagittula* he transferred the species to *Spiroplecta*. This was unfortunate because *T. sagittula* is the genotype of the valid genus *Textularia* Defrance set up in 1824 and according to the Code cannot be transferred to another genus. To make matters worse *Spiroplecta* Ehrenberg 1844 is an *objective junior synonym* of the hyaline planktonic genus *Heterohelix* Ehrenberg 1843, in that it is based on the same genotype, *'Textilina' americana.*

In 1903, Silvestri recognised that Wright's material required a new name and coined one in his honour, accompanied by a description and figures. The species was now properly designated but he continued to use the invalid generic name, *Spiroplecta*. This was not rectified until Cushman (1949) transferred the species to his new genus *Spiroplectammina* set up to include biserial agglutinated species with large initial coil.

These references, leading to what is now considered to be the correct name, are given first.

Spiroplectammina wrightii was now clearly defined but meanwhile Lacroix had reopened the whole question by returning to the view that it was the same as *T. sagittula*. This view was followed by most authors until Loeblich and Tappan redescribed Defrance's species on the basis of a neotype from the Pliocene type locality. These references are given next, followed by (not Defrance) in brackets to make it clear that *T. sagittula* in the sense of these authors is not *T. sagittula* Defrance. The entries could be written, *T. sagittula* sensu Brady etc.

The first record of *S. wrightii* in British waters was as *T. cuneiformis* sensu Williamson. It is interesting that Göes followed this to the extent of regarding the megalospheric generation as *T. sagittula* var. *cuneiformis* but gave a new name to the microspheric generation. Strict application of the 'Law of Priority' would mean that the name *williamsoni* should take precedence over *wrightii* but as explained in the 'Remarks', Göes type is lost and the name has not been used by a subsequent author. In this situation, the International Code which is chiefly concerned to promote the stability of nomenclature allows us to invoke the 'fifty year rule' and reject the name as a *nomen oblitum* (forgotten name). The well-established name *S. wrightii* is therefore left unprejudiced.

The synonymy illustrates very well the tangled nomenclature surrounding certain species of Foraminifera. It is precisely this sort of problem which, although it engages the keen interest of the taxonomist eager to apply 'species law', drives the plain stratigrapher, anxious to use the species in geological interpretation, to complain that taxonomy is concerned not with the species but with a legalistic wrangle over names that do not matter very much.

Such an idea was probably in the mind of the oil company representative who once interviewed me for a job. In order to appraise me of their priorities and as soon as I had sat down at his desk, he said, 'I must tell you that we have no use for a taxonomist'. Fortunately, I had already had some experience in the industry and was quickly able to reassure him and explain that I had every intention of applying my knowledge of Foraminifera in stratigraphy and oil exploration but I also mentioned, as gently as possible, that this very application depended upon sound taxonomic practice.

As was so pointedly remarked by Mayr, Linsley and Usinger (1953), it is simply not true in taxonomy that a rose by any other name smells just as sweet. In the case of *Spiroplectammina wrightii* not only have five different specific and varietal names been applied but three genera have been confused to the extent that a neotype has been suggested for one, *Textularia*, which actually belongs to another genus! Thus on the one hand there has been undue lumping with confusion even at the generic level, while on the other unjustified splitting has taken place due to a failure to distinguish dimorphism from specific differences. It is only when the names of such muddled species are corrected, with strict attention paid to the International Code as well as to the modern species concept, that they can be applied unambiguously and therefore usefully in stratigraphy.

CLASSIFICATION ABOVE THE GENERIC LEVEL

After the recognition of species and the grouping of related forms into genera, the taxonomist is faced with the task of arranging the genera into suprageneric categories of family and order (with intermediate groupings such as subfamily, superfamily and suborder interposed where necessary). This is done on the basis of gross morphological similarities and differences to give an orderly hierarchy that reflects the true lines of descent. The main problem with Foraminifera as with most other major groups of animals is that information is still insufficient for this to be done with any confidence. Major morphological features of the test which where held in common are thought to indicate affinity and a monophyletic grouping may, conversely, have arisen at different times in different groups by adaptive convergence. Emphasis of such features will therefore produce polyphyletic groups and a horizontal rather than a natural, vertical classification. Only detailed stratigraphic and evolutionary studies can solve these problems and as a matter of practical convenience it is necessary to compromise and accept a partly artificial scheme as a working tool.

A brief review of the history of classification in the group will highlight some of difficulties in the way of the attempt to build a genetic system and changing opinions about the value of different morphological characters of the test. N.B. For an exhaustive review of the various classifications that have been proposed the reader should consult Loeblich and Tappan (C140 – C163, 1964).

Although Foraminifera were known in the seventeenth century and were figured by Aldrovandi of the University of Bologna in 1648 and by Hooke who included *Ammonia beccarii* in his *Micrographia* of 1665, the early microscopists were uncertain which class of animals they belonged to. Doubt remained until well into the nineteenth century. They entered scientific literature with the publication of the 10th edition of the *Systema Naturae* of Linneaus of 1758, where fifteen species are listed as *Nautilus*. Interest in the group then increased towards the end of the eighteenth century with publication of works on Recent species from the coast of southern England (Walker and Boys, 1784; Walker and Jacob, 1798; Montagu, 1803, 1808). Recent and fossil species from the Mediterranean and Red Sea (Soldani, 1789, 1795; Fichtel and Moll, 1798) and fossil species from the Eocene of the Paris Basin (Lamarck, 1804). A number of trochospiral, planispiral and uncoiled species were ascribed to *Nautilus* because of the resemblance of the shells to cephalopods, but others were variously classed with worms, echinoderms and even corals. However, a number of generic names were set up, such as *Rotalia, Nodosaria* and *Nummulites* that are still valid.

The idea that the Foraminifera were cephalopods gained strength in the early nineteenth century, and in the earliest formal classification of the group by de Blainville (1825) they were divided amongst the ten families recognised according to shape; thus *Nodosaria* was placed with *Orthoceras*. They were first recognised as a separate order, Foraminifères, still within the Cephalopoda but distinguished by possession of foramina rather than internal siphons, by d'Orbigny (1826) who is justifiably regarded as the 'father of scientific foraminiferal studies'. Five families were distinguished on the basis of chamber arrangement. Within a decade a further major advance was made by another French worker Dujardin (1835), who discovered that they were Protozoa. This was accepted by d'Orbigny in his classification of 1839, where he raised the Foraminifera to a class and recognised six orders on the basis of the chief modes of chamber arrangement, although as late as 1838 the German micropalaeontologist Ehrenberg still thought they were Bryozoa.

Ehrenberg, however, appears to have been the first to point out the presence of perforations (Ehrenberg, 1841). This feature was not applied in classification until Carpenter (1856) showed that certain genera grouped together by d'Orbigny could be separated on the basis of this character. Thus the annular discoid, perforate genera *Cycloclypeus* and *Heterostegina* can be separated from the imperforate *Archaias* and *Orbitolites*. Carpenter supposed there must be a fundamental difference between genera in which the soft parts are in intimate connection through the test wall and others where the only means of communication is through successive foramina to the aperture. This was not immediately related to wall structure but in the Introduction to *Recent Foraminifera of Great Britain,* Williamson (1858) pointed out that three main types of wall structure could be distinguished: (1) opaque calcareous or porcellainous (porcelaneous), rich brown in transmitted light and rarely perforated; (2) calcareous and glassy (hyaline); and (3) agglutinated.

These observations were combined into a comprehensive system by Carpenter, Parker and Jones (1862). Two suborders were recognised, Imperforata, to include membranous, porcelaneous and arenaceous families and Perforata, taken to include a hyaline perforate family, a planktonic family and a family with canals in the walls. A different, more elaborate scheme with 28 families was produced by the German worker Reuss in the same year, but he modified his classification in a postscript, placing his families in Carpenter's major divisions but excluding the membranous forms. These schemes were published only three years after the appearance of the *Origin of Species* by Darwin, in 1859, which brought the idea of evolutionary descent to the fore. It is therefore interesting, at this early date, to find workers in two European countries recognising the problem of convergence in groups of Foraminfera hitherto distinguished by chamber arrangement alone and deciding unequivocally that wall structure and composition were of primary phyletic importance.

These classifications have a decidedly modern ring and it might be thought that the last decades of the nineteenth century would have seen further elaboration of these ideas. But for a number of reasons this was not to be. In part this was because the new classifications presumed a necessary connection between wall structure and perforation, an idea which received a serious blow when Moebius (1880) discovered pores in the wall of the agglutinated genus *Textularia*. In part this was due also to changing ideas about the limits of variation in species. Williamson (1848) carefully distinguished a number of species of *Lagena*, but later he decided they could all be included in one species (Williamson, 1858). With the general acceptance of evolutionary relationships in Foraminfera, Williamson's approach was carried to an extreme by the 'English School' who came to regard the Foraminifera as a simple, very plastic order that could be grouped around a few intergrading basic types and capable of almost infinite variation in response to environmental effects. The classifications of Carpenter and Reuss therefore came to be regarded as overelaborate and artificial.

These changing ideas are well illustrated in the new classification that was proposed by Brady (1884). Brady had worked for a decade on material collected on board the research vessel 'Challenger' during the first expedition to make soundings in all the major oceans of the world (1872 – 74). Many new genera and species came to light in the oozes of the abyssal plains and he found it necessary to set up a new family for unilocular, agglutinating genera (Astrorhizidae) and to retain the Globigerinidae set up by Carpenter, Parker and Jones for planktonic genera. On the other hand, he recognised only 10 families in all, a marked reduction from the 28 families of Reuss. The formal division into Perforata and Imperforata was abandoned and both agglutinating and calcareous biserial genera were included in the Textulariidae. This retreat from the idea of the primary importance of wall structure was carried further by Neumayr (1887) who considered that the major calcareous groups had all passed through an agglutinated stage.

Brady's classification had the virtue of simplicity and backed by the beautiful plates in the Challenger Report has remained in use, modified by Lister (1903), almost into our own day (Jepps, 1956).

A further blow to the idea of the importance of perforation was the discovery by Rhumbler (1895) of pores in the juvenarium of the porcelaneous genus *Peneroplis*. Although it is likely that these 'pores' are homologous with the later multiple apertures rather than true perforations, it destroyed the idea of a necessary connection between perforation and wall structure. It also, inevitably, further weakened the idea of the importance of wall structure in itself.

Evidence now appeared from another quarter which greatly strengthened the hand of the 'English School', this was the discovery of the supposed Cambrian Foraminifera of the Malverns (Chapman, 1900). Casts ascribed to calcareous Foraminifera, including *Dentalina*, had already been found in the Silurian of Wales (Blake, 1876b; Keeping, 1882) and the discovery of well-preserved nodosariids in a limestone thought to be from a band in the White Leaved Oak Shales at Malvern seemed to prove that genera such as *Nodosaria* and *Marginulina* occurred as far back as the Cambrian. Indeed, three of the Foraminifera were placed in species that are still living. This appeared to confirm that not only were the Foraminifera a simple, plastic group but that some species ranged through the entire stratigraphical column. It is not surprising that the application of Foraminifera (particularly smaller Foraminifera) in stratigraphical studies in Britain flagged during the early years of this century, that papers were written emphasising their lack of usefulness (Vaughan, 1923) and that credence could be given to the mechanistic ideas of d'Arcy Thompson *(On Growth and Form*, 1917) who considered that all the shape variations shown in *Lagena* could be explained by physicochemical forces acting on a droplet of protoplasm. The use of wall structure as a character in classification was further devalued and Douvillé (1906a) went so far as to assume that it was determined entirely by habitat. Those authors who did take account of it in classification were almost bound to decide that calcareous forms sprang from tectinous ancestors first and that agglutinating forms arose later and were more advanced (Galloway, 1933; Chapman and Parr, 1936).

This 'stumbling block to confident phylogenetic work' was not removed for almost half a century until the patient detective work of Wood (1947) demonstrated with 'a single shot' that the supposed Cambrian nodosariids were derived from an erratic block of Rhaetic or Lower Lias limestone. A little later Wood (1949b) was also able to show that the supposed casts of Silurian Foraminifera from Cardiganshire were inorganic. No better example could be found of the interdependence of taxonomy and stratigraphy or a more 'awful warning' against collecting from talus without keeping proper records.

So it was that the ideas on classification and phylogeny of the Foraminifera at the turn of the century showed a complete reversal of those prevailing in the middle of the nineteenth century. Fortunately for the growth and development of our science, developments in the economic field at the end of that century were soon to dispel the cloud that had settled on academic foraminiferal studies.

The famous 'Drake Well', the first boring specifically sunk in search of oil, was drilled in 1859, the year of the publication of the *Origin of Species*. For several decades crude oil was used mainly in the manufacture of lamp oil and lubricants, but the invention of the internal combustion engine transformed demand. Even by 1900 there was a considerable export trade from America to Europe. Pennsylvania, the scene of the original discovery, actually reached peak production of over 30 million barrels per annum as early as 1891. After that, production declined. There was thus a constant need to find new fields and this stimulated more scientific methods of geological exploration. The application of foraminiferal studies to subsurface work began with water well borings (Sidebotham, 1866; Jones, 1884; Howchin, 1889, 1891) but was rapidly extended to oil field development.

It is of interest that the first application to correlation of oil wells appears to be the work of Grzybowski (1897) in the Palaeogene of the Potock field in the Carpathians of Poland. This was followed soon after the turn of the century by the researches of Udden in the Illinois and Texas oil fields (Croneis, 1941; Jones, 1956; Stuckey, 1978). So successful was this work in the USA that micropaleontology became established as a formal course in many universities from 1916 onwards, and in the immediate post-war period (1919–21) the oil companies began to employ full-time micropalaeontologists—the first three were in Texas and were all women (Alva Ellisor, Hedwig Kniker and Esther Applin). The value of smaller Foraminifera as index fossils was clearly demonstrated (Ellisor, Applin and Kniker, 1925; Israelsky, 1933) and a great number of new genera and species came to light.

The name chiefly associated with the taxonomic work on this new material was that of Joseph Cushman. He began his career working mainly on Recent Foraminifera but became well known as a consultant to the US Geological Survey and to various oil companies and eventually, in 1924, set up his own laboratory at Sharon, Massachusetts and began the publication of the famous *Contributions on Foraminiferal Research*.

In 1927 Cushman published, 'An outline of a reclassification of the foraminifera'. This was very comprehensive and a great advance, replacing earlier groupings by 45 families which were increased to 50 in the last edition of his book 'Foraminifera' (Cushman, 1948). These families were clearly distinguished on grounds of wall structure, chamber arrangement and aperture character, with coiled genera regarded as leading to uncoiled genera. Fortunately, unlike Galloway, he ignored the supposed Cambrian Foraminifera of the Malverns, following a suggestion of Howell and Sandidge (1933) that they were, probably, originally chitinous. He was thus (like Neumayr) able to regard the unilocular agglutinating group as the most primitive and ancestral to the majority of other Foraminifera. In his views on the importance of recapitulation he followed Lister (1903) and Schubert (1907, 1912) rather than Rhumbler (1895, 1911, 1923) and Douvillé (1906a) who believed that uniserial genera could lead to coiled genera. The families were not grouped in phylogenetic lines (probably because of the difficulties of the stratigraphic evidence), but 15 families of calcareous perforate forms were regarded as having common descent from a rotaliid ancestor. As has been shown by Wood (1949a), apart from *Peneroplis* and its allies which Cushman separates from other porcelaneous forms on the grounds of their postulated, separate, perforate ancestry, his families can be grouped into larger divisions based on wall structure. That this was not done shows the lingering doubts concerning the importance of wall structure and the persistence of the idea of the primary importance of perforation. In addition, the Palaeozoic endothyrids were regarded as agglutinating and included with the lituolids.

An attempt to group the families into phylogenetic lines was made by Glaessner (1945; see reprint 1963a) and seven superfamilies were recognised on the basis of wall structure, chamber arrangement and apertural characteristics:

Astrorhizidea Lituolidea	Agglutinating
Miliolidea	Porcelaneous imperforate
Endothyridea	Microgranular
Lagenidea Buliminidea Rotalidea	Hyaline perforate

The major wall structure groups were therefore recognised as natural divisions with a common origin in coiled, unilocular agglutinated ancestors. Again, fortunately, the mistaken belief of Howell and Sandidge that the Cambrian Foraminifera of the Malverns were calcified, chitinous forms meant that they were ignored. Differences from Cushman's classification include the idea that the fusulines were derived from the endothyrids and that the porcelaneous group are a natural group with a common origin in a coiled unilocular form.

The work of Wood (1947, 1949a) not only removed a stumbling block in the way of recognition of the stratigraphical succession of the major groups of Foraminifera but greatly clarified knowledge of wall structure. The optical characteristics of the main types of wall were clearly defined and in particular the hyaline group was shown to include both radial and oblique ('optically granular') genera. Research into the fine structure of the foraminiferal test now proceeded apace with the assistance of the TEM from the early 1950s and the SEM after 1968. Attention was also directed into the details of the lamellar structure of the hyaline Foraminifera and Smout (1954) suggested there were two distinct groups, one with simple lamellar structure (discorbids) and another with additional septal flaps (rotaliids proper). A third group, with primary double lamellae (bilamellar structure), was distinguished by Reiss (1958, 1963).

These discoveries, together with the great expansion of foraminiferal studies after World War II, soon prompted a number of new classifications of which the most important and most widely followed was that of Loeblich and Tappan (1964) in the *Treatise on Invertebrate Paleontology*. Ninety-five families were recognised, grouped in 17 superfamilies and 5 suborders. Wall structure and microstructure were regarded as the most important features and were the basis for the recognition of the suborders. Apertural characters were considered next in importance and chamber arrangement came third.

(1) Allogromiina (membranous).
    Lagynacea.
(2) Textulariina (agglutinated).
    Ammodiscacea.
    Lituolacea.
(3) Fusulinina (calcareous microgranular).
    Parathuramminacea.
    Endothyracea.
    Fusulinacea.
(4) Miliolina (porcelaneous calcitic).
    Miliolacea.
(5) Rotaliina (hyaline perforate).
    Nodosariacea—monolamellar, radial, terminal aperture.
    Buliminacea—monolammellar, radial, loop-shaped aperture.
    Discorbacea—monolamellar, radial, trochospiral.
    Spirillinacea—monolamellar, single crystal.
    Rotaliacea—septal flap, radial.
    Globigerinacea—bilamellid, radial, planktonic.
    Orbitoidacea—bilamellid, radial, benthonic.
    Cassidulinacea—monolamellar, bilamellid, optically granular.
    Carterinacea—spicular calcite, single crystal.
    Robertinacea—radial aragonite, internal chamberlets.

So, remarkably, we find that after almost exactly 100 years the wheel of opinion has turned full circle and the prime considerations in the classification of the Foraminifera are wall structure and the layering of the test, much as conceived by Carpenter and Reuss but with perforation now subordinate.

History, is again repeating itself, however, in that opinion has already swung away from the extreme position taken in the 'Treatise'. As shown in chapter 4, Towe and Cifelli (1967) have demonstrated that although radial and granular wall structure are distinct optically they are crystallographically close and one may easily give rise to the other. Bellemo (1974b) has shown that intermediate forms exist. Variation apparently occurs at the species level in many families (Haynes, 1956; Wood and Haynes, 1957; Hansen, 1972), so it appears that the superfamily Cassidulinacea is an artificial grouping.

The attempt to subdivide the hyaline Foraminifera on the basis of layering has also run into difficulties largely because of uncertainty in interpretation of observations. Disagreement has arisen particularly over the Globigerinacea, regarded as monolamellar by Hofker (1971) or including both monolamellar and bilamellar forms (Towe, 1971) rather than being solely bilamellar as considered by Reiss. The latest view is that all the Rotaliina, including those forms with septal flap, are bilamellar except the Nodosariacea (Hansen and Reiss, 1972a; Grønlund and Hansen, 1976). It also appears that the septal flap may be of independent origin in different superfamilies (Haynes *et al.,* 1973; Hansen and Lykke-Anderson, 1976).

These difficulties have been taken into account by Loeblich Jnr and Tappan (1974) in a modified version of the 'Treatise' scheme of classification. The attempt to include all the hyaline-oblique genera in the Cassidulinacea is abandoned and this superfamily is restricted to the high trochospiral and enrolled biserial forms. The other families are grouped in the new superfamily, Nonionacea. Similarly, the attempt to group all bilamellid forms in the Orbitoidacea is abandoned. This superfamily is now restricted to the typical, annular complex Orbitoids and the small, trochoid forms are placed in the Discorbacea. On the other hand, the overall grouping of the superfamilies into five suborders on the basis of the major differences in wall composition is retained and as a measure of the continuing expansion of work into the group, the number of families recognised is increased to 119, together with a new superfamily, the Duostominacea, to include several, early Mesozoic, hyaline families.

The attempt to make wall composition the basis of the distinction between the major groups has been carried further by Hohenegger and Piller (1975) who recognise three orders: Allogromiida—naked forms; Textulariida—-agglutinated; and Tournayellida—secreted calcareous. In part, the idea that all the calcareous families are closely related stems from the idea that the uniserial nodosariids (radial-hyaline and lamellar) arose directly from the uniserial members of the Endothyracea (microgranular and layered). This was argued by Brotzen (1963) and has since been generally accepted (Loeblich and Tappan, 1974). However, the evidence is largely circumstantial, relying on the apparent joint occurrence of these groups in the Permian and the suggestion that the radial-hyaline wall of the nodosariids arose by reduction of the layered endothyrid wall to the 'fibrous' layer. Thus Norling (1968) postulated an outer (or even an inner) microgranular layer in Lias nodosariids and argued that the apparently granular costae of *Nodosaria metensis* represented a former microgranular layer.

This suggested relationship appears to represent the continuing confusion between microgranular, fibrous structure and hyaline-radial structure, despite the work of Cummings and Wood (chapter 4) which clearly demonstrated the fundamental differences between them. This confusion partly arises because the term 'fibrous' has been indiscriminately applied, both to columns of microgranules without optical alignment as well as to the stacks of microcrystals in the hyaline groups (well seen in the ultra-thin sections of Conger, Green and Lipps, 1977 and in the etched 'acicular crystallites' of Bellemo, 1974a). Also, it has even been used to distinguish the perforate portions of microgranular and hyaline tests from the imperforate areas.

This notion also represents the continuing confusion between grains or granules (morphological granular structure) and hyaline-oblique structure (optically granular) and overlooks the fact that the wall may be both granular and optically radial. In any case, it appears that the supposed micrógranular layers in early nodosariids are of diagenetic origin (Gerke, 1957; Grønlund and Hansen, 1976) and cannot be used to support the idea of their descent from endothyrids.

Clearly, details of wall structure can only be used in classification at the suprageneric level with great care and with equal attention paid to the other features of test construction. Chief among the other features of the test is aperture form and position and these are made the primary basis for subdivision in the major alternative to Loeblich and Tappan's classification proposed by Hofker (1951) and modified by Reiss (1958). In Hofker's scheme the hyaline Foraminifera (Dentata or toothplate Foraminifera) are regarded as originating in the agglutinating Valvulinidae. This family which is distinguished by possession of a valvular tooth is considered to have given rise to three suborders. The Protoforaminata, including the buliminids, and their allies with a single aperture or protoforamen, toothplate and fine 'protopores'; the Biforaminata, with a second aperture or 'deuteroforamen', as in the Ceratobuliminidae; and the 'Deuteroforaminata', with coarse 'deuteropores' and in which the deuteroforamen is dominant and the protoforamen reduced, marked by a toothplate only, in advanced forms such as the Rotaliidae.

This classification, which postulates a multilocular, agglutinated stage in the ancestry of the hyaline group, recalls the ideas of Neumayr. It also not only makes internal characters of central importance but brings perforation back into consideration. The main objections to it are that until the comparative morphology is better known and the necessary evolutionary studies have been made the proposed relationship of the three suborders must remain hypothetical. The varied toothplates in the different groups may have arisen by convergence and in many cases the recognition of an aperture as a deuteroforamen can only be made on theoretical grounds. It has also not yet been shown that protopores are definitely structurally more primitive than deuteropores.

This brings us back to the theme of the opening paragraph of this chapter: only detailed stratigraphic and evolutionary studies can solve the problems facing the erection of a phylogenetic scheme. In the meantime it seems best to give careful consideration to aperture form and position and chamber arrangement, as well as wall structure, without overstressing any one of these factors as an overall key to suprageneric classification. The basis for the classification followed here is set out in figure 5.3. Although wall structure is retained as the primary basis of

WALL COMPOSITION AND STRUCTURE	ORDERS	COILING MODE	APERTURE FORM	SUPERFAMILIES	STRATIGRAPHICAL RANGE
Agglutinated commonly layered	Astrorhizida	non-septate, globular,tubular or branching	simple terminal	Ammodiscacea	Camb. - Rec.
	Lituolida	planispiral to uniserial or annular	basal median to terminal and multiple	Lituolacea	Carb. - Rec.
		trochospiral	basal ventral to terminal and multiple (may be dentate)	Ataxophragmiacea	Carb. - Rec.
Calcitic microgranular non-lamellar simple to layered	Fusulinida Fusulinina	non-septate, globular or tubular	simple to multiple	Parathuramminacea	U. Palaeozoic
		planispiral to uniserial	basal median to terminal and multiple	Endothyracea	U. Palaeozoic
		trochospiral	basal ventral to multiple	Tetrataxacea	Carb. - Perm.
		planispiral discoid to fusiform	multiple to ? absent	Fusulinacea	Carb. - Perm.
outer hyaline radial layer	Archaediscina	non-septate, tubular, planispiral, conical or winding	simple terminal to stellate	Archaediscacea	Carb. - Perm.
		uniserial and overlapping	terminal, simple or 'radiate'	Colaniellacea	U. Palaeozoic
Porcelaneous layered non-lamellar	Miliolida	biloc. or biloc. to irregular	simple terminal	Nubeculariacea	Carb. - Rec.
		winding with elongate chambers	simple terminal	Ophthalmidiacea	Carb. - Rec.
		planispiral to uniserial or annular	median and multiple	Soritacea	Jur.- Rec.
		winding to uncoiled cylindrical or compressed, or fusiform	dentate terminal to multiple	Miliolacea	Jur. - Rec.
Calcitic hyaline radial mono. or multilamellar	Nodosariida	planispiral to uniserial, unilocular	peripheral to terminal,'radiate'	Nodosariacea	Perm. - Rec.
		alternating to unilocular	terminal,'radiate'	Polymorphinacea	Trias. - Rec.

Aragonitic hyaline radial bilamellar	Robertinida	planispiral to trochospiral	double or umbilical with distal arch and proximal notch	Duostominacea	Trias. - Jur.
		trochospiral	umbilical to marginal or peripheral, narrow toothplate, secondary foramen	Ceratobuliminacea	Jur. - Rec.
		trochospiral to planispiral	umbilical to areal, broad partition, primary foramen	Robertinacea	Eoc. - Rec.
Calcitic hyaline radial or oblique, bilamellar	Buliminida	high trochospiral to biserial, uniserial and unilocular	basal and comma-shaped to terminal with toothplate	Buliminacea	Jur. - Rec.
		compressed or enrolled biserial to uniserial	basal median, marginal or terminal slit, with toothplate	Bolivitinacea	Jur. - Rec.
		triserial to biserial (or enrolled biserial) to uniserial	marginal, subterminal or terminal slit with internal tube (may be lost)	Cassidulinacea	Cret. - Rec.
Calcitic hyaline radial, oblique, compound or single crystal★ bilamellar or with septal flap†	Rotaliida	★ non-septate, or multilocular with 2 or 3 chambers per whorl	simple terminal or umbilical	Spirillinacea	Trias. - Rec.
		trochospiral, umbilicus open or secondarily closed	umbilical to extraumbilical	Discorbacea	Cret. - Rec.
		trochospiral to planispiral & uncoiled or annular, umbilicus closed	extraumbilical to multiple	Asterigerinacea	Cret. - Rec.
		trochospiral to annular or arborescent	ventro-median to medio-dorsal or multiple	Orbitoidacea	Cret. - Rec.
		trochospiral to involute planispiral with retral processes and canals	basal ventral to multiple	Nonionacea	Cret. - Rec.
		† trochospiral to planispiral septal fissures or canals	basal ventral to multiple	Rotaliacea	Cret. - Rec.
		† planispiral with marginal cord and canals or annular	basal median to multiple	Nummulitacea	Cret. - Rec.
Calcitic hyaline radial bilamellar	Globigerinida	trochospiral	umbilical to extraumbilical with asymmetric flaps	Hedbergellacea	Cretaceous
		planispiral to biserial	median with flaps or lip	Heterohelicacea	Cret. - Mio.
		trochospiral or streptospiral	umbilical to extraumbilical with lip, teeth or bullae	Globigerinacea	? Jur. - Rec.
		trochospiral to planispiral	ventro-median to median with extensions or areal	Hantkeninacea	U. Paleoc. - Rec.

Figure 5.3 Wall composition and structure in the orders of Foraminifera and the characteristic coiling modes and aperture forms in the superfamilies

subdivision, I have modified Loeblich and Tappan's arrangement by placing rather more emphasis on aperture form and have returned some way towards the simpler scheme of Glaessner but with the superfamilies raised to orders. In the recognition of a number of orders (with revival of some old names) it follows the course advocated by the 'Russian School', recently restated by Grigelis (1978a) following Fursenko (1959a). However, it differs in two major aspects: greater emphasis on wall structure at the primary level means that 9 rather than 14 orders are recognised, whereas in contrast, 32 rather than 26 superfamilies are recognised because coiling mode and apertural form are given equal weight. Stratigraphical range is also taken into account and it will be seen from the table that there is a general succession of wall structure groups. This provides good evidence of evolutionary development and replacement with time, as noted by Hansen (1979).

SUMMARY

Stratigraphical and ecological work depends upon the precise discrimination of species, defined as interbreeding populations with a distinctive morthology. Polytypic species comprise several related subspecies (informally = 'form'). Similarly, a number of related species, found to be connected by morphological gradients when traced through space and time, are grouped as a superspecies (informally = 'group'). Allopatric speciation is apparently general which, together with the episodic geological record, explains why many foram species appear abruptly in the stratigraphic column.

Species are distinguished largely on chamber shape and quantitative differences in number and volume as added, genera largely on qualitative differences in chamber arrangement, aperture position and tooth structure. Note, however, that in both cases the boundaries between related forms may be gradational. The fossil sample is normally incomplete and environmental and preservation effects must be carefully distinguished from genetic variation.

The features of the foraminiferal test of importance in classification and also those which should be considered in description are as follows:

(1) *Preservation*
Whether: test in its original state or altered, recrystallised, dolomitised or silicified—damaged or collapsed and if so the degree of distortion.

(2) *Habit*
Whether: free or fixed; surface of attachment present.

(3) *General appearance*
Whether: unilocular or multilocular, with relative size and proportions; periphery rounded or keeled.

(4) *Coiling mode*
Whether: planispiral—wound in a horizontal series of whorls; globose or lenticular—involute or evolute.
trochospiral—in a helicoid spiral; high or low, biconvex, plano- or concavo-convex.
uniserial—straight bead-like series—rectilinear, curvilinear or inverted V shape.
biserial—alternating, double series.
triserial—high trochoid with three chambers to each whorl.
quinqueloculine—alternating from end to end, adjacent chambers at 72°, 120° or 180° to each other.
annular—horizontal series of ring-like chambers.
annular complex—lamellar, annular arrangement with lamellae buckled to form lateral chambers.
planispiral fusiform—planispiral with extended axis of growth.
irregular—arborescent, spreading or wild growth.
biform or triform with relative proportions.

(5) *Chambers*
Whether: globose or compressed; high or low; different on each side in trochoid tests and number and size increase as added; increasing in number or decreasing with each whorl; periphery angular, rounded or

produced into a keel; partitions present in annular discoid and annular complex genera; equatorial chamberlets square, rectangular, ogival or prismatic and characters of lateral chamberlets; juvenarium and nepionic ring present; axial or spiral septula present in planispiral-fusiform genera; labyrinthic infolding in agglutinating genera.

(6) *Sutures*
Whether: depressed, elevated or limbate; straight or curved; sigmoid, meandrine or reticulate; different on each side in trochoid tests; spiral suture marked; septum folded in planispiral fusiform genera.

(7) *Wall*
Whether: agglutinated or calcareous; if calcareous, microgranular, hyaline or porcelaneous; thick or thin; layers or lamellae present; if agglutinated, cement calcareous or organic with amount and colour; size and character of adventitious material; pores present with size and shape; canals present in lamellar forms.

(8) *Ornament*
Whether: external surface smooth, spiny or ribbed with coarse costae or fine striae, continuous, broken or localised; umbilical boss present; sutures ornamented with nodes; pillars at corners of lateral chamberlets, along septa or in umbilicus.

(9) *Aperture and accessory structures*
Whether: umbilical, sutural, areal or peripheral; size, position and shape change with growth; single or multiple (cribrate); with neck, lip or coverplate; with internal teeth or toothplate; internal foramen different.

(10) *Measurements*
These should include diameter and height or length. Also, if possible, the size of the proloculus and the rate of increase in size and diameter of the chambers and whorls as added. See chapter 13 for measurements considered important in the Larger Foraminifera.

Application of foraminiferal species in stratigraphy requires unambiguous designation of type specimens and naming according to the Rules of Nomenclature established by the International Committee for Zoological Nomenclature (ICZN) in accordance with the Principle of Priority. The five primary types recognised are Holotype, Syntype, Paratype, Lectotype and Neotype. Subsequent revision and redescription of the species requires construction of a synonymy which gives not only synonyms and the history of generic shifts but also brings together the references that establish the geographical and stratigraphical range.

Classification of Foraminifera at the suprageneric level is based upon wall structure, apertural form and chamber arrangement, taken together with the evidence of stratigraphic range and ontogeny. It is uncertain how far the latest schemes proposed can be considered natural. The history of classification reveals how opinion has swung back and forth between different major features of the test in the search for a 'key' to the origin and relationships of the different groups. At present it seems best not to overstress any one factor and to keep the possibilities of adaptive convergence in mind while working towards a phylogenetic scheme.

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Chapter 6

The Agglutinating Foraminifera

> Tests of agglutinated Foraminifera (are) built by the industry of the protoplasm and we may compare this action with the building of nests by birds or webs by spiders. These ... are so characteristic for the species that (build) them that we could, if necessary, characterise each species by (this) means....
>
> (Hofker, 1972)

The agglutinating group are geographically the most widespread Foraminifera at the present day (Phleger, 1960; Murray, 1973b). As explained in chapter 4, this is because the organic cement binding the foreign particles of the wall allows them to flourish below the calcite compensation depth (CCD) on the abyssal plain, as well as in brackish, marginal marine environments with low alkalinity. This group can also tolerate lower oxygen levels, which allows them to live in silled basins and apparently to penetrate deeper into the sediments than calcareous forams (Buzas, 1974).

The Foraminifera with organic test wall or with a tectin membrane and only a partial agglutinated covering (order Allogromiida) are almost unknown as fossils, so despite their present-day abundance and undoubted importance in the economy of nature they will not be further considered here.

The recently recognised group of non-septate, agglutinating Foraminifera placed in the superfamily Komokiacea by Tendal and Hessler (1977), where the test consists of ramifying tubes, are also extremely important in the deep sea. In certain areas where Foraminifera are the dominant group of meiofauna (animals in the size range 45 μm to 1 mm) the Komokiacea may equal all other groups in abundance. Unfortunately, the tubes tend to disintegrate on death, so members of this group are also unknown as fossils.

Our attention is thus necessarily concentrated upon the agglutinating groups that occur as fossils, the members of the Ammodiascacea within the non-septate Astrorhizida and the multilocular, septate Lituolida (see the Summary Classification at the end of the chapter). Even here, a number of genera are of fragile construction, so these groups are less well represented in the fossil record than at the present day. However, the tectin cement is mixed with organically bound, ferric iron in most genera and with calcium, in addition, in a number of genera living under 'normal' marine conditions. All the eleven genera and species analysed by Hedley (1963) contained iron, including the non-septate, *Astrorhiza limicola, Hyperammina subnodosa* and *Saccammina sphaerica,* as well as the multilocular *Cyclammina cancellata* and *Verneuilina 'polystropha'.* Similarly, all the sixteen genera and species analysed for iron by Murray (1973a) showed a positive reaction including *Lagenammina atlantica, Cribrostomoides jeffreysii, Spiroplectammina wrightii, Trochammina inflata* and *Jadammina macrescens.* Strikingly, calcareous cement was present only in certain normal marine genera, *Gaudryina rudis, Clavulina pacifica, Spiroplectammina wrightii, Pilulina jeffreysii, Protobotellina cylindrica* and *Saccammina sphaerica.*

Hedley regards these inorganic components as 'vital for the stability and complete cohesive quality of the cement' which lead by processes still not fully understood (see Towe, 1967) to the formation of hard, strongly built tests in many genera, some of which are found fossil as far back as the Cambrian.

Although, as has been mentioned, Lipps (1973) considers the supposition that agglutinating Foraminifera secrete iron and calcium to be unproven, it is significant that Murray found pores only in the species which have calcareous cement. The pores are internal and generally have blind ends. They make an anastomosing network in *S. wrightii* and, as in calcareous species, the pores are lined with an organic membrane and are surrounded by the calcite cement which occurs as, 'more or less equigranular grains 0.5 – 0.7 microns in size'. This seems to foreshadow the way the organic tubules are packed in the blocky, sutured units of microcrystals in *Ammonia,* as described by Banner and Williams (1973), and seems to suggest that the calcite is secreted by the foraminifer.

Pertinent to this discussion of the character of the cement in agglutinating Foraminifera is the discovery by Buckley, Easton and Johnson (1974) that encrusting deposits of iron overlain by manganese, occurring in deep-water ooze in the eastern Mediterranean, are apparently preferentially associated with *Rhabdammina.* This is explained as due to the preferred surface for deposition provided by the Foraminifera. However, Greenslate (1974) has also found *Saccorhiza* in association with manganese nodules in a way that suggests the Foraminifera participate in their construction. *Saccorhiza* builds its tubes of ferromanganese micronodules, other mineral grains, radiolaria and sponge spicules which apparently become a framework for the precipitation of ferromanganese hydroxides. These processes may be entirely inorganic but would seem to be related to the composition of the wall and the presence of ferruginous cement in these agglutinating Foraminifera. That agglutinating Foraminifera, especially attached species, may initiate nodule growth by producing an iron-rich layer is also suggested by the work of Dugolinsky, Margolis and Dudley (1977) in the Pacific. The highest density of species (up to 20) is where the nodule is in contact with the sediment, and it is thought that the scavenging action of the forams may help to keep the nodules from becoming buried—a hitherto unexplained phenomenon.

The common occurrence of larger sand or silt grains packed in a matrix of small grains and cement to produce the mosaic structure that has been illustrated for *Eggerelloides scaber* (plate 7, no. 12) prompted the earlier term, 'arenaceous', for this group. The common selection of quartz grains is no doubt related to the fact that Foraminifera not only feed on the bacteria and algae coating these grains but that the surface chemistry of quartz may increase the solubility of iron (Towe, 1967) and is therefore preferred.

CHAMBER FORM AND COILING MODES

The agglutinating Foraminifera include the largest group of genera of non-septate or 'unilocular' forms as well as the second largest order of multilocular forms. Taken together, and even leaving aside the Komokiacea, the Astrorhizida (Ammodiscacea) and Lituolida together show most of the chamber forms and coiling modes known in the Foraminifera as a whole—fourteen of the eighteen modes recognised in Figure 4.3. This makes them by far the largest group and the most varied architecturally.

Astrorhizida

As has already been pointed out just over half of the genera of Astrorhizida are globular (including hemispherical) forms, almost one-third are tubular, while coiled and irregular forms make up just over one-fifth. These differences in chamber forms are taken as the basis for distinguishing the families in the Ammodiscacea: hemispherical to globular in the Saccamminidae, tubular, often branched in the Astrorhizidae and enrolled, often irregularly unwound, in the Ammodiscidae.

The aperture of the test in the Astrorhizidae and Ammodiscidae is usually formed by the open end of the tube and there is more than one where the tube is open at both ends or the tube is branched. The aperture is more restricted in the Saccamminidae and may be furnished with a neck, considerably extended in *Lagenammina* and *Pelosina.* In *Pilulina* it is slit-like.

In some genera the wall is thickened with irregular, alveolar cavities on the interior (labyrinthic structure) as in *Botellina, Schizammina, Oryctoderma* and *Thuramminoides.* This structure has been used to make subfamily and even family distinctions, but it appears in a number of separate lines within the Astrorhizidae and Saccamminidae. Its presence in *Botellina* has also been disputed by Hofker (1972) who regards the interior as simply criss-crossed with sponge spicules. In *Daitrona* the interior is partially subdivided by radial partitions.

The agglutinating Foraminifera build their tests from a wide range of material gathered from the sea floor and even from particles in suspension, and the variety of materials employed is a particularly striking feature of the astrorhizids. This prompts the question of how far the composition and structure of the wall can be used in the classification of this group.

It was pointed out in chapter 4 that genera like *Rhizammina* are non-selective and apparently build their tests from whatever material is most readily available, while others like *Technitella* (the 'little mason') are apparently highly selective. However, the work of a number of authors, including Slama (1954) and Buchanan and Hedley (1960), shows that under tank conditions where the preferred material is not available other

	Thick	Thin	Layers	Sand/Silt	Mud	Spicules	Other	loosely cemented	strongly cemented	cement only between grains	embedded in cement	Colour
Astrammina limnicola	*		2+	2 sizes	*	scattered	forams	*				grey
Astrorhiza arenaria	*		3-4	coarse				*		'inner lining'		grey-brown
A. limnicola	*		1-2	coarse	*			*				grey
A. polygona		*	2-3	fine			forams olivine		*		?	dk grey-brown
Hyperammina elongata	*		2+	variable			blk grns		*	*		red/yellow-brown
H. distorta	*		?	fine		scattered	forams		*		*	light yellow-brown
H. friabilis	*		2+	variable		rough warp & weft oral end		*		'inner lining'		yellow-brown
H. laevigata		*	one	fine					*		*	red/yellow-brown
H. spiculifera	*		several			rough warp & weft		*		*		yellow-brown
Bathysiphon albus	*		several			warp & weft			*		*	white, dull
B. filiformis	*		several			rough warp & weft			*		*	white
B. flavìdus	*		several			warp & weft			*		*	yellow-white
B. rufus	*		several	minute rounded		?			*		*	red & polished
Marsipella elongata		*	two	fine		tile-like		*				yellow-brown
Psammosphaera fusca	*		one	coarse					*			yellow-brown
P. testacea	*		one				forams		*			grey
Rhabdammina abyssorum	*		several	fine to med					*	*		brown
R. linearis	*		several	fine		scattered	dk grns		*	*		brown
R. radiata	*		several	fine, 2sizes					*	*		grey to yellow
R. triangularis		*	one	variable				*		'inner lining'		brown
Saccammina sphaerica	*		2+	fine		few aboral			*	*		yellow-brown
Technitella legumen	*		several			warp & weft					partially	white

Figure 6.1 Wall structure in selected genera and species of agglutinating Foraminifera. Data from Hofker (1972)

particles may be substituted, even perspex or glass, with mixtures of markedly different sizes. In addition, Smith and Kaesler (1970) statistically analysed the size, shape and mineralogy of sand grains in *Reophax curtus* from the Barents Sea and found that the grains were virtually indistinguishable from those in the sediment. They concluded that the species only showed selectivity in choosing larger sand grains for its later chambers. However, they did admit that, even at stations where up to one-third of the sediment consisted of sponge spicules or other dead Foraminifera, none was used, whereas *R. spiculifer* invariably uses spicules to the exclusion of other material. Thus although selectivity is plastic in *R. curtus* the restriction to sand grains indicates genetic control.

Hofker (1953, 1972), after studying astrorhizids recovered from over wide areas of the North Atlantic (Danish Ingolf Expedition 1895 – 96), the Caribbean (Mortensen Expedition 1914), the Pacific (Mortensen Expedition 1914 – 15) and the Mediterranean, considers that most species in nature are highly selective. He believes that species can be recognised both on the character of the material used in the wall and in the way the particles are bound to determine its fine structure. He also believes that the species can be arranged in genera and even subfamilies on the same basis, although there are always species that differ from the typical.

The table in Figure 6.1 has been prepared from Hofker's data. This illustrates not only that there are clear differences between species but that on the whole the generic groups are also clearly distinct. Thus species of *Bathysiphon* are generally built of sponge spicules embedded in cement, whereas species of *Rhabdammina* are generally strongly built of quartz grains with cement only between the particles. There is rather less consistency within the *Hyperammina* group, which leads Hofker to suppose it may comprise more than one genus. It will be noted that the wall is usually of two or more layers and that it is often compound with different sizes and arrangements of the particles in the layers.

The spicular species, in particular, seem mainly to prefer a warp and weft structure in which the inner layer is generally arranged across the length, while the outer layer is arranged parallel to the length, sometimes in a tile-like fashion. This appears to combine strength with light architectural construction.

Hofker's results indicate that some species may be limited to substrates with their favoured sizes and types of material, but on the other hand a species such as *Technitella legumen* which is built entirely of sponge spicules does not change its character when living in the Caribbean rather than the North Atlantic. Species of *Reophax* are always composed of a single layer. *Hyperammina elongata* which is built of several layers of sand grains occurs together with *H. spiculifera,* built of layers of sponge spicules. Further, *H. novaezealandica* from the South Pacific differs from *H. spiculifera* in its tile-like rather than simple, longitudinal arrangement of spicules on the exterior.

The very common occurrence of spicules in the walls of astrorhizids may be because they are protective in a group made up largely of sedentary suspension or deposit feeders (see chapter 4), especially when they are held out at an angle to the surface or jut out around the aperture as in *Halyphysema.* It is also possible that they are more easily gathered from suspension when the species is epiphytic, as in the case of *Technitella,* when it is attached to seaweed such as *Fucus.*

Another feature illustrated by the table in figure 6.1 is that an obvious 'inner lining' is only apparent in the case of loosely cemented forms. This illustrates very well that it is the tectin which becomes the cement between the particles in the strongly cemented species (or the cement in which the particles are embedded).

Some of the simple tubular genera come superficially close to the agglutinated shells of other invertebrate groups, in particular to the tubes of some polychaete worms. However, in most cases polychaete tubes are horny or leathery, markedly tapered and only roughly agglutinated. Strongly built, sandy tubes closest to foraminiferal tests are constructed by Pectinaria. These are open at both ends and constructed of clean sand or shell, but can be distinguished from *Bathysiphon* by their more flaring form, composition and lack of a layered, compound structure. The agglutination of larger silt grains flat on to the surface packed in a matrix of finer grains and cement, as in *Eggerelloides* (plate 7, no. 12), seems to be characteristic of arenaceous Foraminifera. Also characteristic is the way the cement may coat the outer surface, almost embedding the grains, as in *Reophax arcticus* (plate 7, no. 10). Here the lip of the aperture seems entirely made up of cement (plate 7, no. 7).

Species built entirely of spicules may be confused with sponges and indeed *Technitella* and *Halyphysema* were originally described as such by early workers (see Hedley, 1958). The problem that may be faced is well illustrated by the difficulty found in deciding the affinities of what appeared to be a new species of *Technitella, T. teivyensis* from Cardigan Bay (Haynes *et al.*, 1973). This species is illustrated by means of a stereopair in plate 9, nos. 9:9. The test is cylindrical and rises from an encrusting base (attached to *Fucus*) tapering slightly to the aperture. The wall is an open network of sponge spicules, generally directed forward at about 45° to the axis of growth and markedly brushed forward around the aperture (plate 9, no. 4).

The arrangement of the spicules in *T. teivenysis* is different from that in the genotype *T. legumen* where, as has been noted, there is a compound warp and weft arrangement with the outer layer longitudinally arranged and partially embedded in cement, well shown in the stereopair (plate 9, nos. 2:2). In addition, broken off specimens (resembling rabbits' tails) occur in dredge samples in Cardigan Bay, together with broken pieces of what does appear to be a true branching sponge (plate 9, nos. 1:1). Despite the fact that close-ups of the wall by SEM (plate 9, no. 8; cf. also nos. 6 and 3:3) seemed clearly to show an agglutinated wall in *T. teivenysis,* was it, possibly, also a sponge?

At this point I felt it necessary to call in a sponge specialist, and Miss S. M. Stone of the Porifera Section at the British Museum of Natural History kindly looked over the material. She agreed that the broken, branched specimens (nos. 1:1) were sponges because the spicules are triradiates arranged in the typical manner of calcareous sponges (Calcarea). The branching form suggested the genus *Leucosolenia* or *Clathrina.* Turning to *T. legumen* (Brady's material in the BM) she noted that the acicular spicules are tylostyles (knobbed at one end and pointed at the other) with the knob ends projecting outwards in many instances, not inwards as in sponges. Similarly, she noted that the spicules in *T. teivyensis* were set in position in an unnatural way and agreed that I was probably correct in considering it a foraminifer and different from Norman's species *T. legumen.* However, she pointed out with justification that only a study of its life history would settle the question. Unfortunately, we have not yet been able to do this.

Lituolida

More than 200 genera of multichambered, agglutinating Foraminifera are recognised. They exhibit most of the known coiling modes and, as can be seen from figure 4.3, high trochospiral/uniserial genera are most numerous, making up some 40 per cent. If we group high trochospiral/uniserial with biserial/uniserial and solely uniserial together (on the supposition explored in chapter 4 that these modes indicate adaptation to an infaunal life) this figure reaches 56 per cent. Low trochospiral arrangement is relatively uncommon, 7 per cent. It is significant that the percentages for these groups in the Rotaliida are almost exactly reversed. Leaving aside the conical lituolids this would seem to be a clear indication of radically different life strategies in these two orders. Planispiral to uncoiled genera (excluding biserial) are also an abundant group, reaching 19 per cent. Planispiral agglutinating genera are common in the deep sea probably as deposit feeders, the strong trends to uncoiling and uniserial growth again, possibly, indicating adaptation to infaunal life along many lines. Interestingly, discoid genera reach 8 per cent, slightly more than in the Miliolida where they generally appear to be shallow water (turbulent zone) forms adhering closely to the sediment or other substrates and to plants as epiphytes. Perhaps the agglutinated wall affords an advantage for life under conditions that are similar but more restricted by turbidity, low temperature or abnormal water chemistry.

Two major superfamilies can be recognised—a planispiral group, the Lituolacea, and a trochospiral group, the Ataxophragmiacea. Families within the Lituolicea are founded on differences in the pattern of chamber development. The chambers become uncoiled and uniserial or annular in the adult forms of advanced Lituolidae, uncoiled-biserial to uniserial in the Textulariidae. The main morphological trend in both these families is towards uncoiling, coupled with changes in the position of the aperture which may be single or multiple. Both cylindrical and blade-like forms are common. Annular growth is achieved in the Lituolidae, and *Dicyclina* has two layers with radial partitions. Labyrinthic structure is again well developed along a number of separate lines with partitions also in *Spirocyclina.* These have been closely studied by a number of different workers, with recognition of a number of separate subfamilies (in particular, Maync, 1952; Voloshinova *et al.*, 1959). These have been critically reviewed by Banner (1970) in a beautifully illustrated paper in which the family name Spirocyclinidae (= Loftusiidae) is revived for them. However, as Banner considers the subfamilies to be of polyphyletic origin (see figure 6.2) it is thought preferable to retain these groups within the Lituolidae.

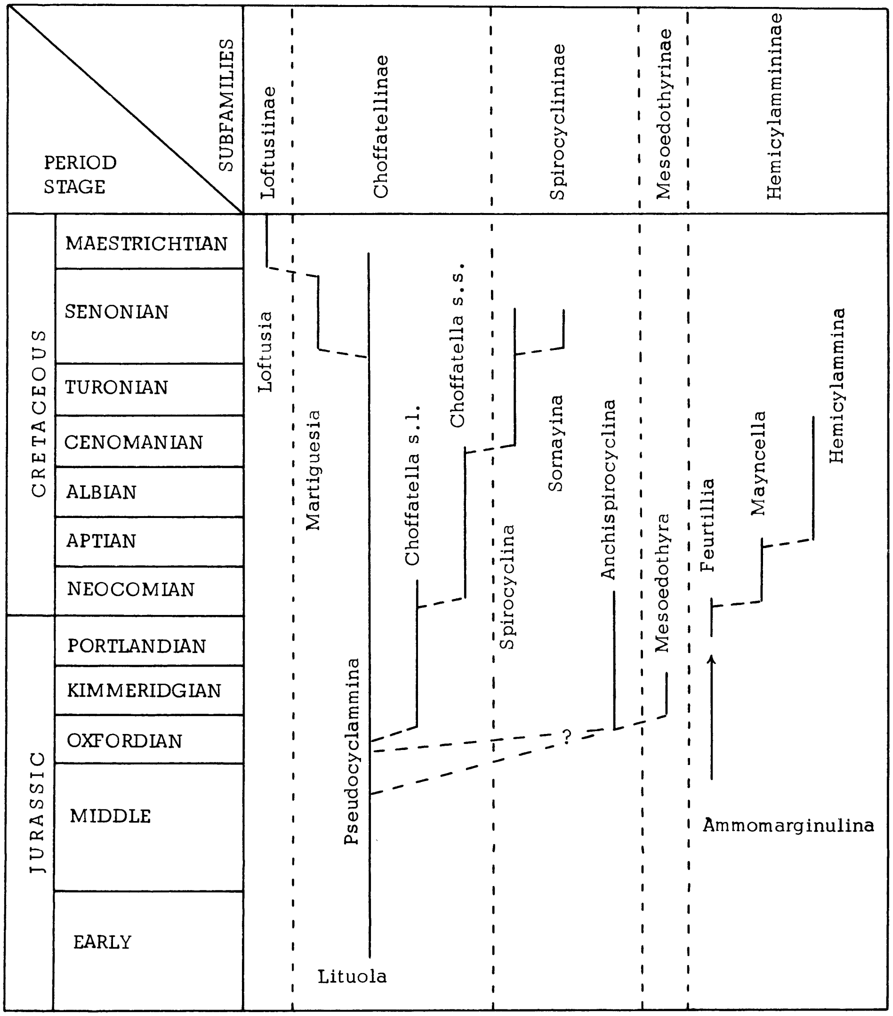


Figure 6.2 **Phylogeny of labyrinthic lituolids in the Mesozoic according to Banner (1970),** ***Revta esp. Micropaleont.*****, 2(3):243 – 290**

The trend towards uniserial growth is equally striking in the Ataxophragmiacea which again show this development along a number of different lines, distinguished by differences in the form of the aperture. The aperture remains simple in the Verneuilinidae, is areal to multiple-terminal with a lip in the Eggerellidae, is furnished with a valvular tooth in the Valvulinidae and becomes a high arch with internal tooth in the Ataxophragmiidae. The Orbitolinidae are asymmetrical-trochospiral to uniserial-conical with multiple apertures.

Internal chamber partitions developed from buttresses or pillars are particular features of advanced members of the Verneuilinidae, the Ataxophragmiidae and the Orbitolinidae. In addition, the Ataxophragmiidae include a subgroup with thickened umbilical zone or 'columella'.

Advanced forms in these families appear to use increasing amounts of calcareous cement in their walls, with a calcareous epitheca in *Orbitolina;* but further work is required to established the detailed structure and composition in most genera and even whether pores or internal tubules are present.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

Although the fossil record of the unilocular Ammodiscacea is patchy and incomplete, they are the first group of Foraminifera with a hard test to appear in the stratigraphic column and are present in the Cambrian. Indeed, the oldest, solid-shelled fossils in the basal, Lower Cambrian of northern Europe belong to the simple, tubular, genus *Platysolenites* which is close to *Bathysiphon* and an index to the Baltic Stage (Glaessner, 1977). There are also spherical forms close to *Psammosphaera* (Howell and Dunn, 1942). Although crushing, distortion and recrystallisation makes precise identification of these forms with Recent genera doubtful, their early occurrence supports the idea that the unilocular Astrorhizida are the most primitive group and probably arose from the Allogromiida via intermediate forms with partial agglutinated coverings. The presence of Foraminifera in the Precambrian is regarded as improbable by Glaessner and, further, the problematical Cambrian calcareous microfossils, *Renalcis* and *Chabakovia,* considered Foraminifera by Riding and Brasier (1975), are dismissed as algae.

Both the Astrorhizidae and the Saccamminidae become much more abundant in the Ordovician with the appearance of *Hyperammina, Rhabdammina, 'Marsipella', Tholosina* and *Hemisphaerammina* (Bykova, 1956; Conkin and Conkin, 1965). Enrolled tubular genera appear in the Silurian, so all the families are present by the end of the Lower Palaeozoic and the foraminiferal faunas achieve considerable diversity and include *Glomospira, Ammodiscus, Turritellella, Lituotuba* and *Thurammina* (Conkin and Conkin, 1977). These agglutinating faunas are particularly well known from subsurface work in the Midcontinent region of the USA following the pioneer work of Moreman (1930, 1933) who obtained material by leaching limestone with hydrochloric acid. Subsequent work has led to the recovery of more than 100 species, with particularly rich assemblages in the Niagaran and its equivalents in Ohio, Indiana, Illinois, Oklahoma and Kansas (Stewart and Priddy, 1941; Miller, 1956; Ireland, 1966: Mound, 1968). Silurian Foraminifera are less well known from other parts of the world but have been described from the Baltic region (Eisenack, 1954) and Austria (Kristan – Tollmann, 1971).

Despite the abundance of the ammodiscids in the Silurian, their rarity in earlier periods means that their phylogenetic relationships remain hypothetical. Possibly the globular saccamminids are the most primitive. They may have arisen from allogromiids with tent-like coverings and, in turn, by extension of the apertural neck into a tube (or tubes) have given rise to both the straight and enrolled tubular forms.

As in the case of the Astrorhizida, the fossil record of the Lituolida is patchy and incomplete although, similarly, their abundance at certain levels demonstrates that they have been particularly favoured at certain times—during the Upper Palaeozoic, when the lituolids appeared, in the late Mesozoic, especially during the Cretaceous when this group reached maximum diversity, and during the Palaeogene.

The planispiral Lituolacea are well represented in the Carboniferous. They may have originated from *Ammodiscus*, the line of descent giving first *Trochamminoides*, with irregular chambering and then *Haplophragmoides*, with regular, involute chambers. These developments may have already taken place in the Devonian. Uncoiled genera are also abundant in the Carboniferous, but labyrinthic structure apparently does not appear until the Jurassic. The Textulariidae may not have appeared until the Mesozoic, either, since the work of Cummings (1955, 1956) shows that most, if not all, the genera supposedly belonging to this group in the Carboniferous are microgranular.

The septate, uniserial *Reophax* is present in the Devonian of the Midcontinent region of the USA. This could be taken to indicate that it arose separately from the Ammodiscacea via *Hyperammina* which may show growth constrictions resembling incipient septa. However, Hofker (1972) considers these constrictions quite different from true chamber formation. Also, it is likely that *Reophax* is polyphyletic and has arisen many times as a result of uncoiling along a number of different lines and quite probably from *Ammobaculites* which is present in the Carboniferous. Resolution of this problem requires further work on Devonian faunas.

The Trochamminidae also appear in the Carboniferous, represented by *Trochammina*, with simple, basal aperture (N.B. doubtful record for the Silurian by Stewart and Priddy, 1941). This genus may also have descended from *Trochamminoides*. Well-preserved Neogene material reveals a number of genera distinguished by areal, peripheral or umbilical apertures. It is likely that these modifications were present in the *Trochammina* stock at an early date, giving rise to most of the typically, high trochospiral families in the Mesozoic and the Eggerellidae in the Cenozoic (although *Mooreinella* Carb. and *Digitina* Perm. may represent early members of the *Eggerella* group related to *Plectotrochammina*).

An explosive development of new genera of Lituolacea took place in the late Jurassic and Cretaceous, many with labyrinthic structure or partitions (see the Summary Classification at the end of the chapter). As stated above, Banner (1970) regards the labyrinthic Lituolidae to be of

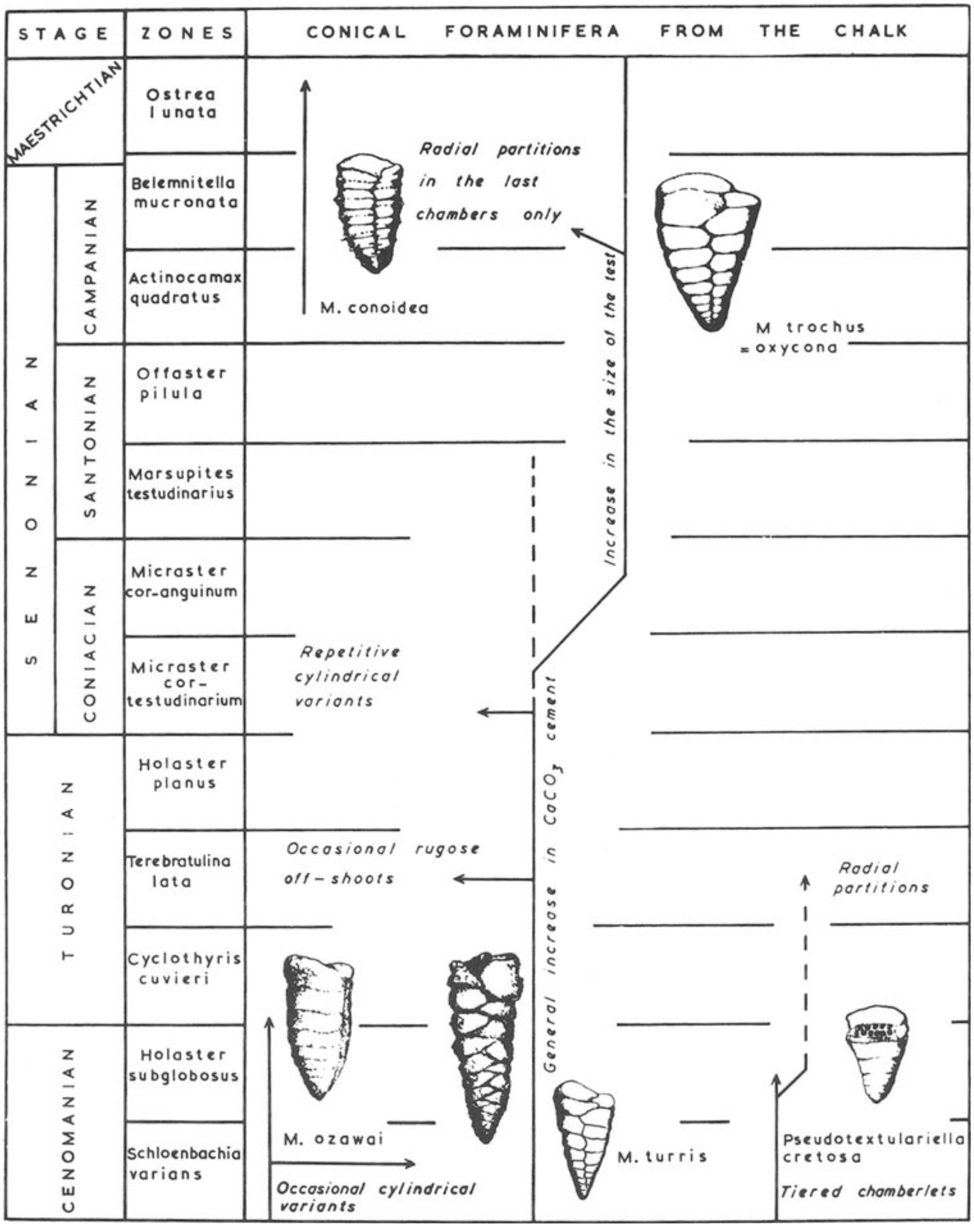


Figure 6.3 Evolution of conical verneuilinids in the Upper Cretaceous. From Barnard (1963a)

polyphyletic origin; the Cretaceous genera being derived from the uncoiled, labyrinthic allies of *Lituola* (*Pseudocyclammina*) and from *Ammomarginulina* or *Ammobaculites*; and Cenozoic *Cyclammina* being derived directly from *Haplophragmoides* via *Cribrostomoides* and *Alveophragmium*. However, on general grounds (see chaper 5) it is considered unlikely that uncoiled genera give rise to close-coiled forms and it is therefore considered more likely that the Cretaceous, *Choffatella* group was also derived from *Haplophragmoides* but independently in the late Jurassic.

The great Cretaceous expansion is also well shown by the Verneuilinidae and the Ataxophragmiidae which are the dominant, high trochospiral families of the Ataxophragmiacea in the Mesozoic and occur from the Triassic onwards. *Verneuilina* probably gave rise to *Gaudryina* in the late Triassic and to *Dorothia* and its close relative *Marsonella*, with flattened apertural face and summit, in the L. Cretaceous.

Barnard (1963a) has shown how *Marsonella* may have given rise to *Pseudotextulariella* in the Upper Albian and to *Textulariella* much later in the Miocene (figure 6.3). *Gaudryina* may also have given rise to *Spiroplectinata* in the Albian and *Verneuilina* to *Tritaxia* which in turn appears to have been ancestral to *Clavulinoides* in the Palaeocene.

Genera of the Ataxophragmiidae, with high loop-shaped apertures, are present by the Jurassic and forms resembling *Arenobulimina* but with thickened central core, such as *Pfenderina* and *Kornubia*, occur from the late Jurassic of the Tethyan Region (Henson, 1948). These were placed in a separate family, Pfenderinidae, by Smout and Sugden (1962) but are best regarded as a subgroup of the Ataxophragmiidae. *Arenobulimina* is abundant in the Lower Cretaceous of N. W. Europe and apparently gave rise to *Ataxophragmium* towards the top of the Albian (Barnard and Banner, 1953).

The history of the Valvulinidae in the Mesozoic is less well documented. Indeed, Barnard (in Barnard and Banner, 1953) pointed out that he had not observed *Valvulina* in his work on the Jurassic and that Mesozoic records probably belong to other genera. However, *Valvulammina* is present in the Lower Cretaceous of the Alberta Trough, Canada.

The development of the Orbitolinidae may have begun with *Kilianina* which occurred as early as the Bathonian in France (Pfender, 1933) and ranged to the Maastrichtian in Arabia (Henson, 1948). This genus is trochospiral to uniserial and conical in form with lamelliform buttresses in the central zone. It is therefore close in structure to *Lituonella* and *Pseudolituonella*. These genera seem to lead logically to the more complex orbitolines which are therefore regarded as one family, following Moullade (1965). Members of this group, some reaching up to 1 cm diameter, became extremely common in the shallow waters bordering the tropical Tethyan sea-way and in mid-latitudes of the Americas (Dilley, 1973).

The different views that have been put forward on the evolution of *Orbitolina*, which defines the Aptian to Cenomanian interval, are an interesting example of the different interpretations that can be put on the same material (figure 6.4). Thus Rat (1963) considers that *Orbitolina* exhibits reticulate evolution with a marked trend from high, conical *O.ex.gr. conulus* to the flattened, discoid *O.ex.gr. concava*. As indicated by the right-hand side of figure 6.4, this is associated with a move from calcareous to sandy substrates. In contrast, Hofker Jnr (1963, 1966a, 1966b) believes there is one lineage, leading through 5 'form-groups', separable on the structure of the juvenarium, to *O. conulus*. But Schroeder (1975) recognises three lineages (given the status of subgenera) descending from *O. lotzei* at the Lower/Upper Aptian boundary.

Although most of the labyrinth and partitioned genera died out by the end of the Cretaceous, a number, including the Orbitolinidae, persist until the end of the Eocene. New labyrinthic genera such as *Cyclammina* and *Alveophragmium* appear in the Palaeocene, possibly representing an independent development from *Haplophragmoides*. Further, besides the appearance of the Eggerellidae, the Tertiary is marked by the incoming of new, high trochospiral Valvulinidae, such as *Clavulinoides* in the Palaeocene and *Cribroturretoides* and *Cylindroclavulina* in the Oligocene. New genera such as *Cribrogoesella* continue to appear in the Neogene and even as late as the Quaternary (*Dusenburyina*).

THE AGGLUTINATING FORAMINIFERA IN STRATIGRAPHY

Although a number of agglutinating genera have a long time range, the continuous evolutionary record of the group since the Cambrian and the bursts of new genera and species in the Silurian and Upper Palaeozoic, the late Mesozoic and the early Tertiary, mean that the 'first appearance' of many forms is of stratigraphic value.

Miller (1956) and Ireland (1966) have shown that fossil remains of this group are of sufficient abundance and diversity in the Silurian to allow subsurface correlation between wells in Kansas on the basis of faunas obtained from acid residues of ditch cuttings. Formations can be dated to Epoch level when a dozen or so species are present and they are particularly abundant in the limestones of the Hunter Group. This work has been carried further by Mound (1968) who has recovered 82 species from the Silurian of Indiana, the Salamonie Dolomite being very rich. He has been able to recognise three assemblage zones, namely Turritellella, Ammodiscus/Thurammina and Ammodiscus/Lituotuba, in ascending order in the uppermost Silurian.

The ammodiscids continue to be important as stratigraphic indices in the Upper Palaeozoic, despite the rise to dominance of the Fusulinida. As shown by figure 6.5, they can be used to define the boundary between the Devonian and the Carboniferous and that between the

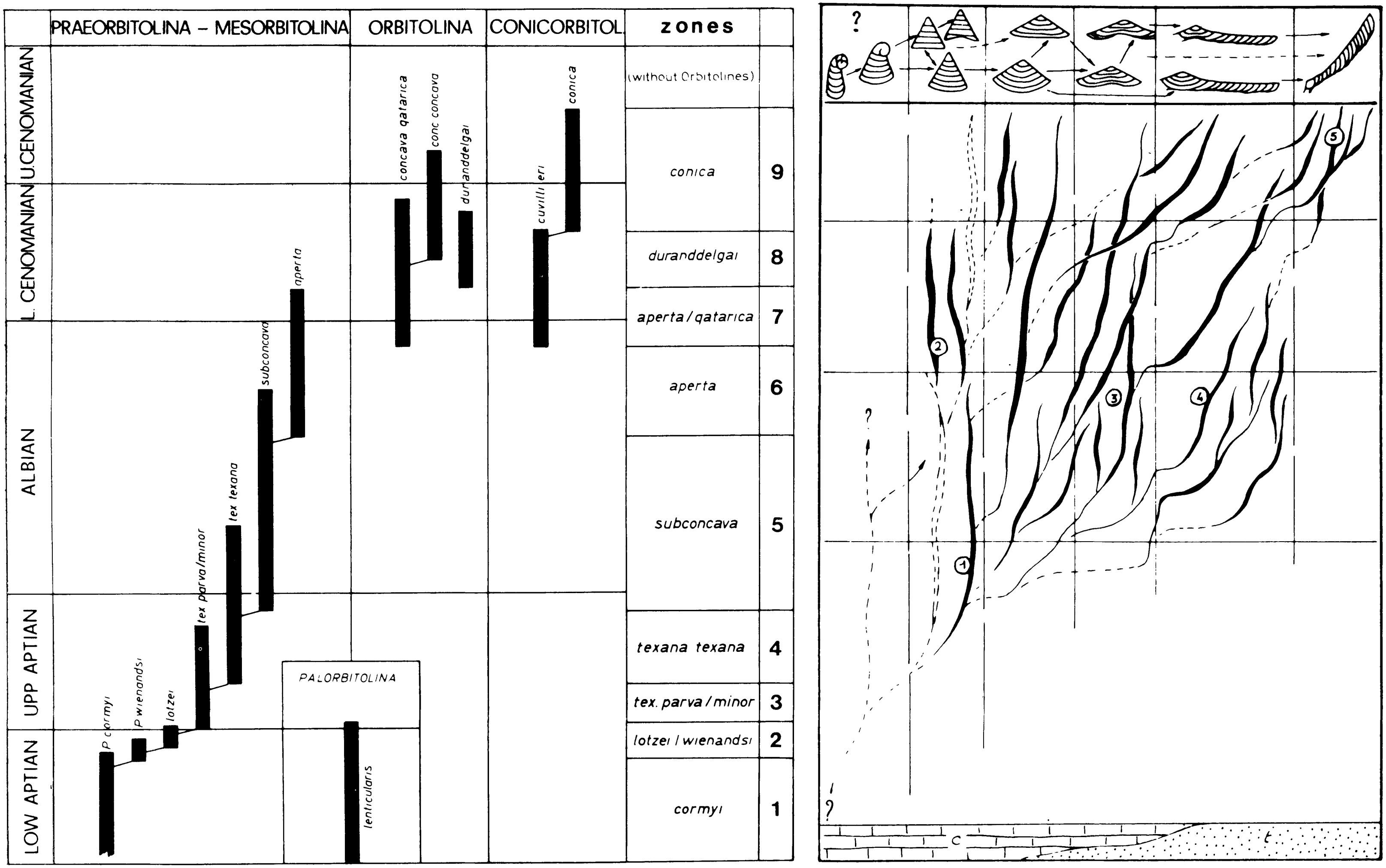


Figure 6.4 Differing views on the phylogeny of the orbitolines. Left, according to Schroeder (1975), *Revta esp. Micropaleont. Num. Esp.*, 117 – 128; right, according to Rat (1963)

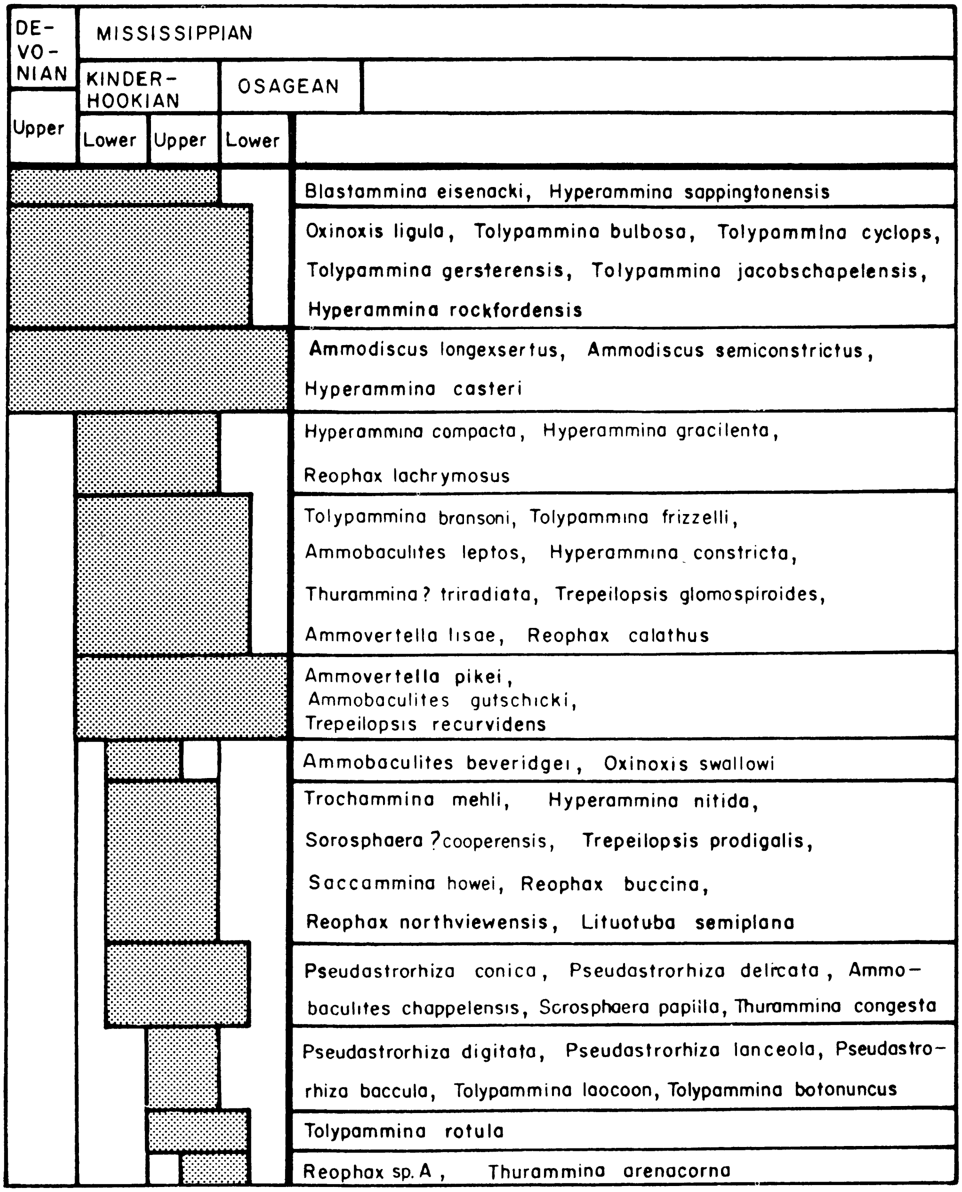


Figure 6.5 Ranges of ammodiscids in the Upper Palaeozoic of the USA, showing their zonal value based on first appearances. From Conkin and Conkin (1977)

Kinderhookian and Osagian within the Lower Carboniferous.

In the late Mesozoic it is the more complex labyrinthic and partitioned lituolids, many of quite short time range, that are valuable as index fossils, as is well shown by figures 6.3 and 6.4. The Orbitolinidae are particularly important in Lower Cretaceous (Moullade and Peybernes, 1975; Schroeder, 1975) and extend into the Palaeogene.

In the Cenozoic the astrorhizids are overshadowed by the calcareous groups but a number of the new genera that appear are nevertheless valuable as stratigraphical markers. In particular, *Clavulina, Martinottiella* (= *Multifidella*) and *Alvarezina*, as well as the longer ranging *Textularia* and *Bigenerina*, have been shown to have stratigraphic utility in the subsurface, Neogene of the Gulf Coast, USA (Leutze, 1972). Leutze notes that careful washing of ditch cuttings is required if these forms are to reach the micropalaeontologist in an identifiable condition.

ECOLOGY

Despite the abundance and undoubted stratigraphic utility of the agglutinated Foraminifera at certain levels, it must be admitted that they are generally subordinate to calcareous genera in most assemblages. Even where they are the dominant element they often consist of long-ranging, simple forms, prone to collapse on burial.

It is a curious fact of the history of foraminiferal studies that the agglutinated group was involved in the pioneer application of Foraminifera to subsurface, oil field work by Grzybowski (1897). He found that they are the dominant group in the Palaeogene sandstones of the producing horizon of the Potock and Krosno fields in the Polish Carpathians. The difficulties experienced by Grzybowski, in attempting to build a zonal scheme on the basis of collapsed and distorted specimens, led to the idea that this group was of little value in stratigraphy. It also, incidentally, checked progress in applied studies in Europe, while work forged ahead on the abundant, calcareous foraminiferal assemblages of the Cretaceous and Tertiary formations of the south-eastern USA.

This idea was still current when I went to work for Shell Oil Company in the Western Canadian Sedimentary Basin in 1954 and began a study of the Cretaceous Foraminifera. Agglutinated Foraminifera proved to be the most abundant element in the microfaunas of the sections examined—sometimes the only group present, which led to some discussion of the usefulness of the project. Fortunately, the early researches of Wickenden (1932), Nauss (1947) and Stelck and Wall (1954) had already shown that a number of the agglutinated species, for example *Miliammina manitobensis*, were extremely useful index fossils in local and intra-regional correlation. It was also understood by this time that microfaunas dominantly, or wholly, composed of agglutinated species indicated peculiar ecological conditions (Glaessner, 1945, reprint 1963a). This promised to be the most interesting aspect of the study for applied micropalaeontology, because it could lead to a better understanding of the palaeogeography and thus to the location of oil reservoirs.

The diagrammatic cross-section (figure 6.6) summarizes the results of the study, confirmed and extended by later, more detailed work, particularly that of Wall (1967), Chamney (1973), North and Caldwell (1975) and Stelck (1975). It is based on a number of boreholes to give a N.E. – S.W. section across Southern Alberta, from the Sweetgrass Arch to the Foothills of the Rocky Mountains. As shown by the key, the microfaunal data are expressed in simplified form as foraminiferal facies, based on dominance of the major wall structure groups, or of planktonic as against benthonic species.

Although not shown on the diagram, some fourteen foraminiferal associations can be distinguished, only three based on calcareous species and only two of these with abundant planktonics. This compares closely with the sixteen recognised by North and Caldwell (1975) in the Cretaceous of Saskatchewan, only two with abundant planktonics and all the others composed, either entirely of agglutinated species or of mixed calcareous benthonic and agglutinated species. This underlines the clear dominance of agglutinated Foraminifera. The facies with only members of this group present are particularly prominent.

How are these unusual assemblages to be interpreted? The normal procedure in palaeo-ecology is to compare fossil faunas with their modern counterparts and to interpret past conditions in the light of present-day distributions. This can only be done with precision if the fossil species are still living (extant). In the case of extinct species we are reduced to comparisons at the generic or family level which then, necessarily, become much more generalised. Also, as pointed out by Stelck (1975), the ecological relations of these Cretaceous foraminiferal assemblages 'are difficult to assess by modern analogy as completely arenaceous suites with a wide spectrum of component elements are rare in modern seas'. It is therefore, possible that precise equivalents of these assemblages do not exist at the present day.

It must also be kept in mind, in palaeo-ecology, that groups of organisms tend to change their habitats with time. Community relations are dynamic and competition and evolutionary changes lead to expansion or contraction of the range. For instance, the sediments and associated faunas indicate that the abundant ammodiscid microfaunas of the Silurian in the American Midcontinental region occupied a variety of shallow marine, benthonic niches (Mound, 1968). Their dominance is attributed by Conkin and Conkin (1977) to their early evolution and pioneer occupation of this environment. It contrasts with their contracted range in later periods after the rise of the calcareous Foraminifera.

There is also the problem of post-depositional alteration of the faunas with possible leaching out of the calcareous tests or reduction of the ferric iron to the ferrous state weakening the tests of the agglutinated forms. The possibility that solution of calcareous tests may explain the dominance of agglutinated Foraminifera in many Cretaceous formations has impressed Scheibnerová (1974). However, Eicher (1977) considers that although the sparse, low diversity microfaunas may in part be due to solution, in most cases they reflect limiting environmental factors. The presence of associated calcareous fossils in the faunas of the Western Interior appears to rule out extensive leaching, although sometimes the calcareous species are preserved only as pyrite casts. Again, leaching can hardly be an explanation of the highly diverse, agglutinated assemblages. The agglutinated species, although often distorted, appear to be generally secondarily silicified and are therefore well preserved.

In order to see just how far a comparison with modern, agglutinating assemblages is informative in the interpretation of the microfaunas of the western Interior, it is necessary to give a brief summary of what is now known about the distribution of Recent forms.

As has been pointed out, the organic cement in the agglutinating Foraminifera and their ability to build their tests of siliceous grains means that they can live under conditions of lowered salinity, alkalinity and oxygen levels. Thus, in Recent seas, microfaunas dominantly or wholly composed of agglutinated species are characteristic both of marginal marine conditions and of deep-sea bottoms undersaturated in calcium carbonate. On the other hand, agglutinated faunas reach their maximum diversity in clear, well-oxygenated waters of moderate (shelf) depth (Cushman, 1935). In particular, this applies to the larger, more complex forms, although *Cyclammina* and its allies are dominant bathyal (Bandy, 1960a; Banner, 1970). However, on the shelf and upper slope the agglutinated species are generally overshadowed by the calcareous genera. In contrast, the agglutinating faunas of extreme environments are generally composed of simple genera able to flourish where calcareous genera are excluded.

As shown by Lowman (1949) in his classic paper on the microfauna of the Mississippi Delta, agglutinating faunas are a particular feature of the delta-front (topset beds). They are also typical of estuaries and tidal marshes. In his review, Murray (1971a) shows that hyposaline marshes (brackish, with salinities < 30 per thousand) are high in agglutinated species with some hyaline species but generally with no porcelaneous forms. Normal marine marshes are also high in agglutinated species with some hyaline and porcelaneous species. Hypersaline marshes (salinities > 35 per thousand) tend to show a mixture of all three groups. Figure 6.7 shows how agglutinating faunas dominate the highest levels of the Dovey marshes almost completely and are the predominant element above the Mean High Water Springs mark.

The main genera in the marginal marine zone are simple lituolids. These include species of *Trochammina, Jadammina* and *Haplophragmoides,* generally with thin, fine-grained walls and prone to collapse. They appear to occur as surface feeders and to some extent as infauna. Definite members of the infauna are the, generally, more coarsely built *Reophax* and the uncoiled *Ammobaculites,* together with *Miliammina* (Buzas, 1974; Frankel, 1975). A number of the species, especially those characteristic of marshes, appear to be cosmopolitan (Phleger, 1967; Scott and Medioli, 1978).

The abundance of large, unilocular ammodiscids and simple lituolids in the deep sea has been known since the voyages of the research vessels Lightning (Carpenter and Thomson, 1868), Porcupine (Carpenter *et al.*, 1869) and Challenger (Brady, 1884), but it is only recently that the distribution of these forms has been mapped in any detail. Exclusive, or almost pure, agglutinated faunas occur below the CCD and are a feature of the trenches and adjoining, deeper parts of the abyssal plains: Kuril-Kamachatka Trench (Saidova, 1961; 1970), Aleutian Trench (Patsy Smith, 1973), Peru Trench (Bandy and Rodolfo, 1964). The general relation to depth is well shown by Patsy Smith's results which reveal an almost entirely agglutinating fauna in the Aleutian trench, a mixed agglutinating/calcareous fauna on the adjacent deep-sea plain and a dominantly calcareous fauna on the Alaskan Terrace. The agglutinating fauna includes a high proportion of tubular forms, interpreted as suspension and deposit feeders as well as passive carnivores (see chapter 4) including *Bathysiphon, Hyperammina, Astrorhiza* and *Rhabdammina*. Uniserial lituolids, including *Reophax,* probably infaunal, are particularly abundant and *Haplophragmoides* and *Trochammina* again occur, as in the marginal marine zone.

Brouwer (1965) has recorded the occurrence of similar, '*Rhabdammina*' faunas in the Cretaceous and Tertiary Flysch of Central and Southern Europe, intercalated with turbidites containing transported, shallow water species including *Nummulites*. These include the difficult faunas studied earlier in the Polish Carpathians by

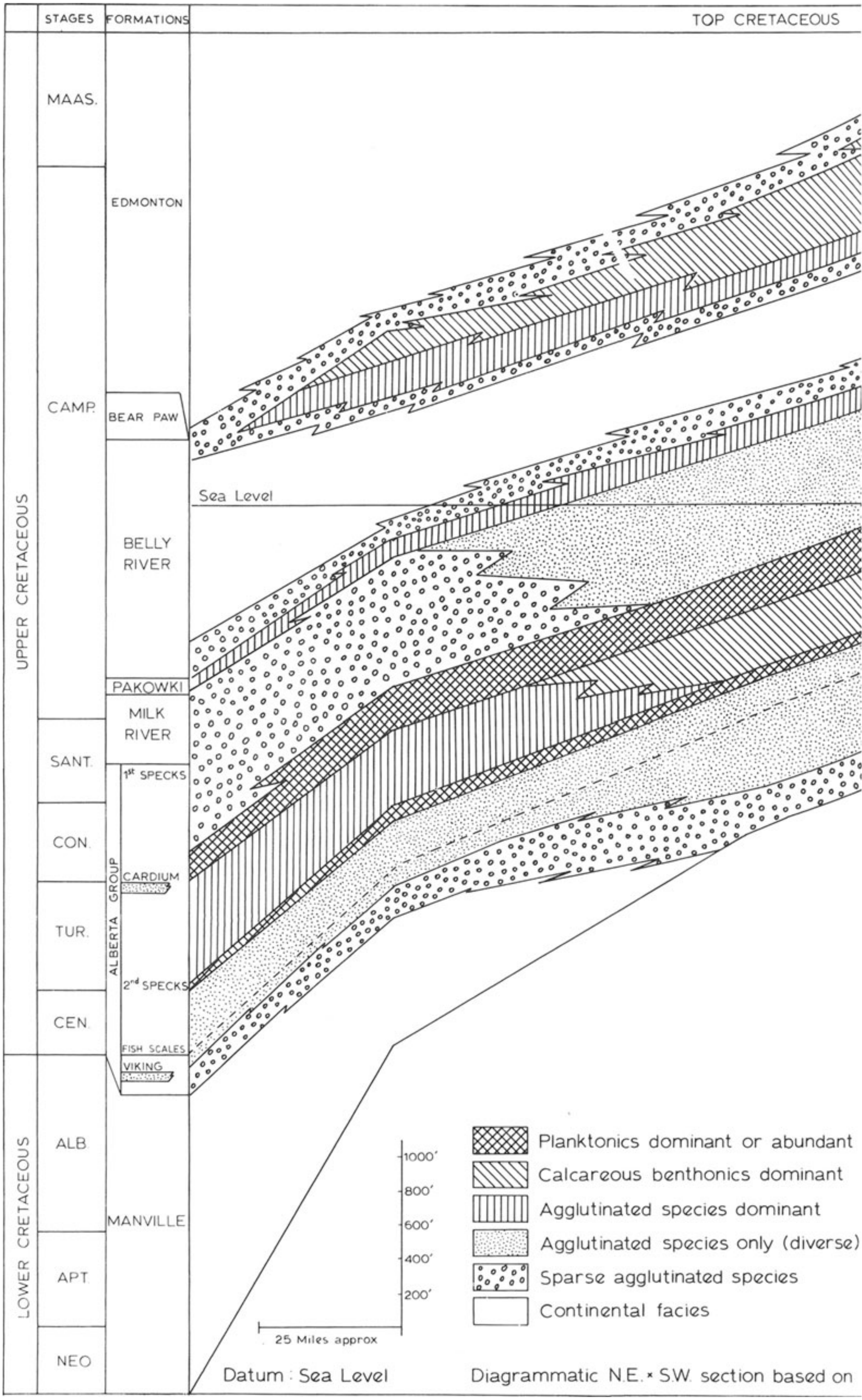
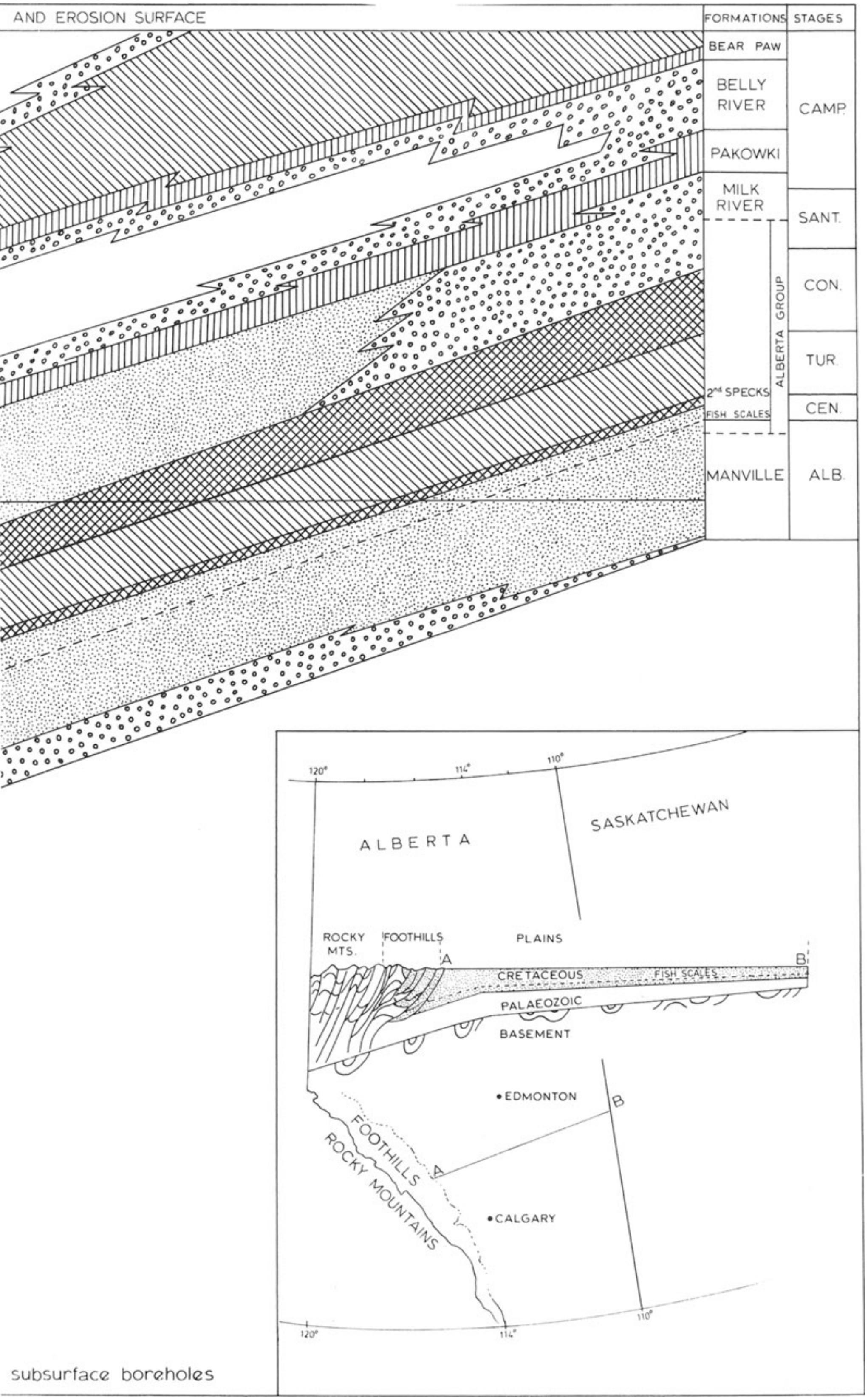


Figure 6.6 **Foraminiferal magnafacies in the Cretaceous of the Alberta**



Trough, Canada (from the Foothills, A, to the Saskatchewan border, B)

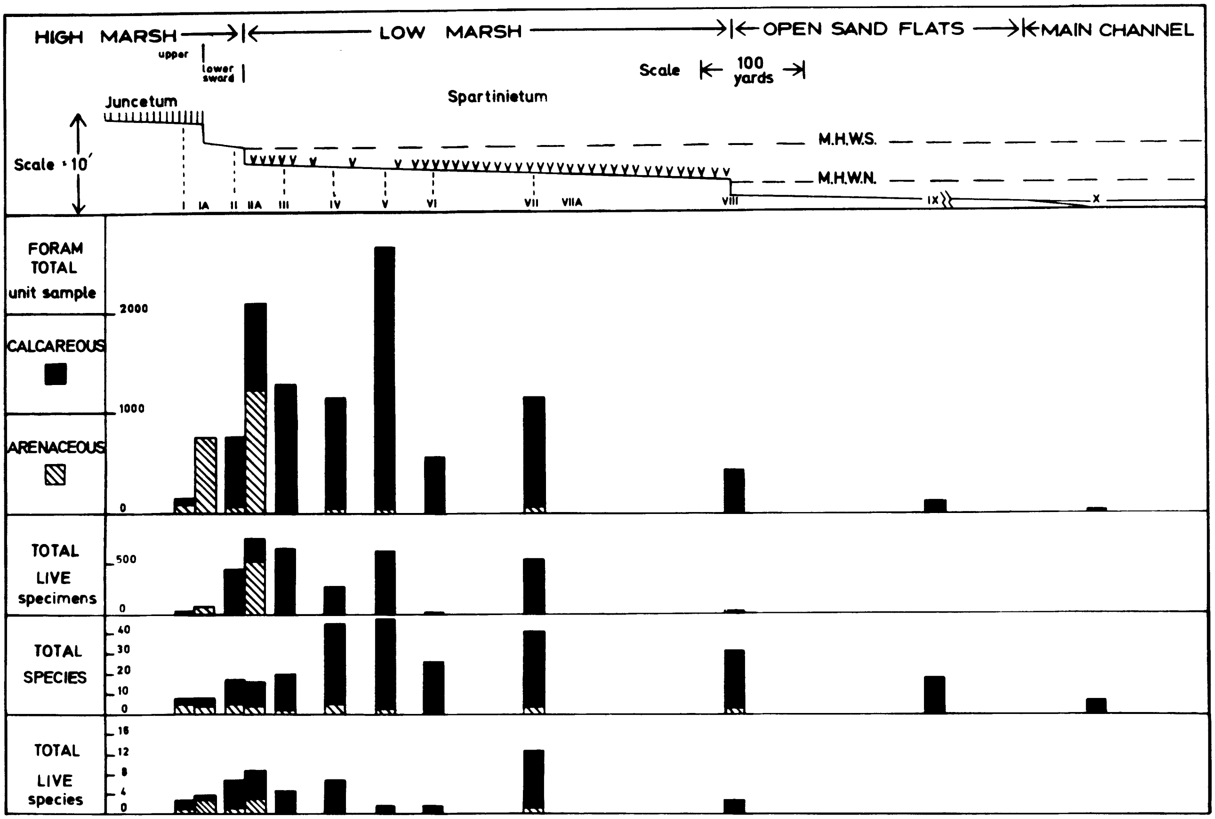


Figure 6.7 Diagram showing how agglutinating (arenaceous) Foraminifera replace calcareous species as the dominant group on the high marsh of the mid-estuary of the river Dovey (Wales). Agglutinating Foraminifera similarly replace calcareous species on the low marsh towards the river end of the estuary where low salinities and alkalinities prevail. From Haynes and Dobson (1969)

Grzybowski and more recently by Geroch (1959, 1960) and Sandulescu (1972). By direct analogy with the present day, these *Rhabdammina* faunas are interpreted as indicating abyssal depths. However, Brouwer admits there are differences from modern abyssal faunas in that the unilocular ammodiscids are relatively more abundant in the Flysch. This may support Stainforth's opinion (1952) that turbidity is the major factor favouring agglutinated Foraminifera in the Flysch environment. A further difficulty is that the CCD is not simply depth and pressure controlled but relates to temperature, organic productivity and perhaps other factors (Berger, 1975; Leroy and Hodgkinson, 1975). In the southern part of the N.E. Atlantic, for instance, mixed faunas continue to depths below that normal elsewhere because the CCD is depressed and the calcareous species *Cibicides lobatulus* and *C. refulgens* are found attached to *Bathysiphon* tubes at 4000 m (Gooday and Haynes, in progr.). On the other hand, agglutinating assemblages are dominant (more than 50 per cent of both living and dead) on the slope in the Sea of Japan (Ishiwada, 1950; Matoba, 1976). Here, although the water is highly oxygenated, low temperatures and relatively low salinities, 34.0 – 34.1 per thousand, together with high levels of organic matter in the sediment, apparently result in low alkalinity which induces dissolution of the dead, calcareous tests. This led Matoba to emphasise the role of the water mass rather than depth, in determining the character of benthonic assemblages (following Phleger, 1964). It is also clear that the *Rhabdammina* fauna, with its large element of deposit feeders and infauna, is strongly substrate controlled. According to Pearce (1980) this fauna is restricted to the areas of Globigerina Ooze in the Rockall Trough and is therefore only indirectly related to depth.

In general the agglutinated assemblages of the Cretaceous of the Alberta Trough are dominated by *Haplophragmoides, Trochammina, Ammobaculites* and *Miliammina*, suggestive of marginal marine sedimentation. At certain levels the faunas are more diverse and include a large number of verneuilinids, as well as *Bathysiphon*. These faunas appear to represent greater depths but because they include extinct genera, like *Tritaxia* and *Spiroplectinata*, their interpretation is more controversial. However, although they include *Bathysiphon*, they differ in important respects from the '*Rhabdammina*' fauna, lacking both *Rhabdammina* and *Hyperammina*.

In these circumstances it is a reasonable course to relate the foraminiferal facies to the palaeogeographic picture built up from general stratigraphical research. Thus according to Rudkin (1964) and Williams and Stelck (1975), the uplifted Cordillera (Nelson and Omineca Uplifts) became a continuous landmass in the early Cretaceous and the source for thick prisms of coarse, paralic sediments which were built out eastwards into a 'shallow epicratonic sea'. Episodic uplift of the Cordillera continued through the Upper Cretaceous and produced four, further, major deltaic cycles recognisable throughout the Western Interior (Hancock, 1975). Throughout this period, as concluded by Williams and Burk (1964), the interior sea remained shallow.

The total Cretaceous sediments form a great wedge, increasing from over 3000 ft (900 m) in thickness at the Saskatchewan border to over 8000 ft (2400 m) in thickness in the western Foothills. The continental and deltaic sediments, including red beds and abundant coals, are the thickest and in the west, where the inter-fingering marine beds tend to thin out, make up most of the section. As is well brought out by the fence diagram (figure 6.6), the facies characterised by agglutinated Foraminifera, together with the continental and alluvial facies, include the major part of the total sediments.

Despite the fact that the microfaunal analysis is based entirely on ditch cuttings and the simplified way in which the results are given, with inevitable loss of detail and completeness, figure 6.6 is consistent with the classic cyclical model for Cretaceous sedimentation in the Western Interior, involving 'large scale intertonguing of marine and non-marine rocks' (Hatcher, 1904; Waage, 1975). If it is assumed that the enormous spreads of deltaic sediments were built out into a shallow interior sea, restricting circulation at the same time as high run-off reduced salinities and alkalinities, the pattern of foraminiferal facies can be related empirically to the major cycles as follows:

Sparse Agglutinated Species (intercalated with coals and plant beds)—delta front (topset beds) with reduced salinities.

Agglutinated Species Only (diverse)—prodelta or inner neritic (foreset beds) with reduced salinities and lowered oxygen levels.

Agglutinated Species Dominant (mixed assemblages)—prodelta or inner neritic, slightly reduced salinities and oxygen levels.

Calcareous Benthonics Dominant — prodelta or inner neritic, normal marine.

Planktonics Abundant — offshore (bottomset beds) moderate depth, normal marine but tendency to foul bottom water.

During the Lower Cretaceous the sea transgressed from the Arctic, with progressive onlap over the continental deposits, reaching southern Alberta in the early Albian. At this time there were no Pacific elements (Jeletzky, 1971). Final marine inundation occurred in the late Albian (*Miliammina manitobensis* zone) when the sea transgressed south and west to the area of the Crowsnest Volcanics and deposited the lower shales of the Alberta Group. This late Albian sea is often referred to as the 'Mowry Sea' from the equivalent Mowry Formation in Wyoming.

The progress of this Lower Cretaceous marine transgression is well shown by the fence diagram (figure 6.6). The continental beds of the Manville are overlapped by the delta front facies (Sparse Agglutinated Species) with interbedded coals and are finally succeeded by the siliceous, restricted, prodelta facies of the Mowry Sea. Researches by Wall (1967), Chamney (1973) and Stelck (1975) prove the wide geographical extension and constant, exclusively agglutinated foram facies of this sea. A prolonged standstill, during which a nektonic fish fauna flourished near the surface and became preserved in the anaerobic muds on the sea bottom, probably accounts for the 'Fish Scales' marker horizon at the Albian/ Cenomanian boundary (Neogastroplites Zone). During the Cenomanian the restricted sea persisted in southern Alberta but became markedly regressive in the north, with the building out of the Dunvegan Deltas from the west (Williams and Burk, 1964).

The transgression which initiated the first cycle of the Upper Cretaceous began towards the end of the Cenomanian and reached its maximum in the early Turonian, with the deposition of the Greenhorn carbonates in the USA. In the more restricted conditions of the Alberta trough, this marine phase is represented by shales speckled with coccoliths, the '2nd Specks' marker horizon of the Alberta Group, interpreted as bottomset beds accumulating at moderate depth (Planktonics Abundant). The regressive phase is represented by the Cardium Formation in Central Alberta and the proximity of the delta front to the line of section is indicated by the facies with agglutinated species dominant. This passes eastwards into the normal, marine facies (Calcareous Benthonics Dominant).

The second cycle began in the early Coniacian with transgression of a sea of moderate depth (Planktonics Abundant) over the Cardium Delta. Although this marine flooding continued elsewhere through the late Coniacian into the Santonian, to achieve maximum inundation of the Western Interior with deposition of the Niobrara Chalks in the USA, the regressive phase began early in southern Alberta. According to Williams and Burk (1964) this was due to uplift in the northwestern USA. This is clearly indicated by the facies diagram where the '1st Specks' horizon, equivalent to the Niobrara Chalks, proved impossible to identify. Regressive sands then built out from the west (Sparse Agglutinated Foram Facies) intercalated with coals in the Milk River Formation. In the east, the same foram facies reflects deposition of the Medicine Hat Sands which accumulated along the flanks of the Sweetgrass Arch. The seaway thus became narrowly confined and the offshore facies gave way once more to the restricted facies (Agglutinated Species Only).

The third cycle began in the early Campanian with the transgression of the Pakowki Sea into the western Foothills area. A mixed assemblage (Agglutinated Species Dominant) indicates a prodelta (foreset) environment and the close proximity of the delta front. During the Middle Campanian, marked regression occurred and the continental and deltaic Belly River Group (including abundant coals) filled the Alberta basin and extended into Saskatchewan, intertonguing with marine members to the north-east (Shaw and Harding, 1954).

The last major transgression of the Upper Cretaceous was represented by the Bearpaw Sea which initiated the fourth cycle in the late Campanian and again reached west to the Foothills area of southern Alberta. As indicated by the fence diagram (figure 6.6), a mixed assemblage (Agglutinated Species Dominant) gave way laterally and vertically to less restricted, normal marine conditions (Calcareous Benthonics Dominant) prior to the final infilling of the basin with the deltaic and coal-bearing formations of the Edmonton Group.

It is therefore apparent, that, despite the generalised form of the diagram, the 'magnafacies' indicate reasonably well the phases of the successive cycles. Work based on continuous cores may eventually reveal microfaunal parallels to many of the lithofacies units of Kauffman (1969), 12 per cycle, 10 seaward of the delta front. Thus detailed work on a cored section of the Bearpaw and adjacent formations in the Strathmore Well, just north of the line of section (Wall *et al.*, 1971) reveals the following sequence: Uppermost 20 ft (6 m) of the Belly River Group, with sparse agglutinated fauna = shallow, brackish, estuarine; Bearpaw, 92 ft (28 m), with agglutinated Foraminifera dominant = inner neritic, depth under 20 ft (6 m); Junction with Edmonton Group, 5 ft (1.5 m), with thin-walled agglutinating species = salt marsh; Transition Zone of lower Edmonton Group, 278 ft (85 m), with intermittent, sparse agglutinated fauna = coal swamp with intercalated, brackish water facies.

Despite the fact that the detailed work of Wall and his co-workers also strongly supports the idea of a shallow interior sea and that the litho-facies analysis of Kauffman (1969) and Kauffman *et al.*, (1977) suggests a maximum depth of 200 ft (61 m) for the carbonates and 500 ft (152 m) for the shales of the Greenhorn and Niobrara cycles, this has not won complete acceptance. Indeed, at the time I completed my own foraminiferal analyses (1956) it was even being suggested in some quarters of the industry that the Cardium sands were deep-water turbidites—although the pebbly sandstone beds of that formation bear no resemblance to classic turbidites but closely resemble shallow water beds of the British Tertiary, such as the 'Hertfordshire Pudding Stone'.

Since that time a lively debate has continued concerning the depth of deposition of the marine beds. In contrast to Kauffman, Asquith (1970) interpreted the Niobrara in the Wind River region of Wyoming as a slope deposit representing some 2000 ft (610 m) depth. Similarly, Frush and Eicher (1975) suggest slope depths of 200 – 1200 m (656 – 3937 ft) for the Greenhorn of the Big Bend region of Texas and Mexico. They explain the meagre or absent benthonic microfaunas of the planktonic facies as due to an oxygen minimum layer, as in the present Arabian Basin of the northern Indian Ocean. By extension of this argument, slope depths are also suggested for the Western Interior.

However, the dominance of continental and marginal marine facies in the Alberta Basin seems to show that sedimentation took place under very shallow or sub-aerial conditions for most of Cretaceous time. If we consider that the subordinate marine formations are a genetically related part of the sequence, that is, if we accept the full implications of Hatcher's cyclic interpretation, it is difficult to envisage a depth of deposition of more than a few hundred feet for any of them. Lowered salinities and alkalinities with foul bottom waters can, on this basis, be explained as a result of the barriers to circulation caused by the growth of imbricate, delta systems in a narrow seaway.

The tendency for workers to consider the depth connotations of particular formations in isolation, illustrates their continuing reluctance to accept in full Hatcher's theory of the west to east oscillation of facies belts which we should characterise today as alluvial, delta front, prodelta and offshore marine. A fascinating account of early opposition to Hatcher's ideas is given by Waage (1975). Plainly this opposition still continues, nor is it confined to geologists working in the Western Interior. A similar groundswell of opposition has built up in the last two decades against the interpretation of the north-west European Tertiary (Palaeogene) as the product of cycles of deltaic sedimentation.

In attempting to arrive at a standpoint of his own, the student should consider that not only is delta formation the major element in sedimentation in most epicontinental seas but that, as is readily explained by plate tectonic theory, truly deep water sediments are rare, except in the subduction zone where 'flysch' is characteristically developed, or on foundered fragments of passive margins.

As we have seen, agglutinated Foraminifera of the '*Rhabdammina*' fauna are, indeed, characteristic of the cool, turbid, deep water, flysch deposits of 'eugeosynclines' and this facies has been identified in northern Alaska (Tappan, 1957) and, in particular, in the Albian of the northern Yukon (Chamney, 1976) where deposits in the Blow River area, with abundant *Bathysiphon*, are interpreted as indicating a 'fore-deep' at the western continental edge of a mobile plate. After a general analysis of the Foraminifera of the Albian of Arctic America (85 per cent agglutinated) and a study of the major morphological groups, illustrated by ingenious, 'morphogroup' symbols, Chamney has abandoned his (1973) idea of a restricted, boreal, Mowry Sea in that area. He now considers that the sea stretched over the entire Cordillera and he now regards the supposed western shoreline of earlier workers as the edge of the shelf and the top of the slope.

Can the results of this reappraisal of the Arctic Albian be applied in the Western Interior, in support of those workers who envisage slope depths for the Alberta Group and its equivalents? It seems unlikely, because it is difficult to reconcile the idea of open access to a western ocean with the apparent requirement of a western source for the huge, Cretaceous prism of largely continental and marginal marine sediments in the Alberta Trough, unless we suppose that for short periods, the positive Cordilleran areas were carried down to oceanic depths. As pointed out by Hancock (1975), the Rocky Mountain Trough shows little resemblance to a eugeosyncline.

It would also make it more difficult to explain the presence of the exclusively agglutinated foram facies. Chamney regards the dominantly agglutinated faunas of the Arctic Albian as normal marine and ascribes the scarcity of calcareous genera to high, silica-bearing, run-off from the continental interior. The abundance of uniserial lituolids, uncoiled genera and high trochospiral verneuilinids is taken to indicate low energy environments of the outer shelf and slope. However, in the Alberta Trough the exclusively agglutinated foraminiferal facies appears to pass laterally into the delta-front facies and laterally and vertically into mixed facies. This facies pattern is better interpreted as a fluctuating response to the growth of deltas in a narrow seaway. We may suppose that apart from restricting circulation and lowering salinity by high upland discharge, the forested deltas contributed large amounts of organic material to the sediments, further reducing oxygen levels and favouring the 'benthonic stagnant', agglutinated faunas found on 'black plant muck' by Lowman (1949). Infaunal agglutinated forms such as *Ammobaculites*, *Reophax* and *Miliammina* may be considered to have had a natural competitive advantage on quiet sea bottoms inclined to oxygen depletion and calcium deficiency below the surface, even where aeration was sufficient for calcareous microfaunas to survive at the sediment – water interface. When restriction became more severe it produced the exclusively agglutinated faunas typical of the Mowry Sea, possibly with *Haplophragmoides* as one of the main, surface deposit feeders. The 'hinge point' between this sea and the open-marine, boreal ocean is considered to have been in the Peel Plateau region of the Yukon (Chamney, 1978).

This discussion indicates some of the problems that face the micropalaeontologist in the use of the Foraminifera in palaeo-ecology. However, despite the controversy over depth interpretation which arises because foraminiferal distributions, like those of other organisms, are only indirectly related to depth (see further the review paper by Funnell, 1967) it is clear that agglutinated Foraminifera can be of great value in environmental interpretation—particularly as useful information can be obtained from ditch cuttings. The student should also note that the fence diagram of foraminiferal facies also brings out another feature of great significance for the oilman; this is the location of stratigraphical traps in clastic sequences formed by sand pinch-outs in shale. These oil and gas traps are coincident with the facies change from delta-front to restricted prodelta deposits and occur particularly in the Manville, Cardium, Medicine Hat and Belly River Formations.

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SUMMARY CLASSIFICATION

In the Summary Classification given below, the authorship of the various taxonomic categories is not given except for names introduced since publication of the 'Treatise' (Loeblich and Tappan, 1964) because they can be found there. Established stratigraphical ranges of the genera illustrated are given and also those of the related genera mentioned when this is different. None is given where the related genus has the same range. The Summary Classification is illustrated with key figures drawn by the author after the type figures (or good figures by subsequent authors) and in the case of internal views of Larger Foraminifera from photographs of thin sections. The original authors are credited in all cases and as I have made particular use of the new material illustrated in the 'Treatise' the authors' names are abbreviated from Chapter 7 onwards (as L. and T.).

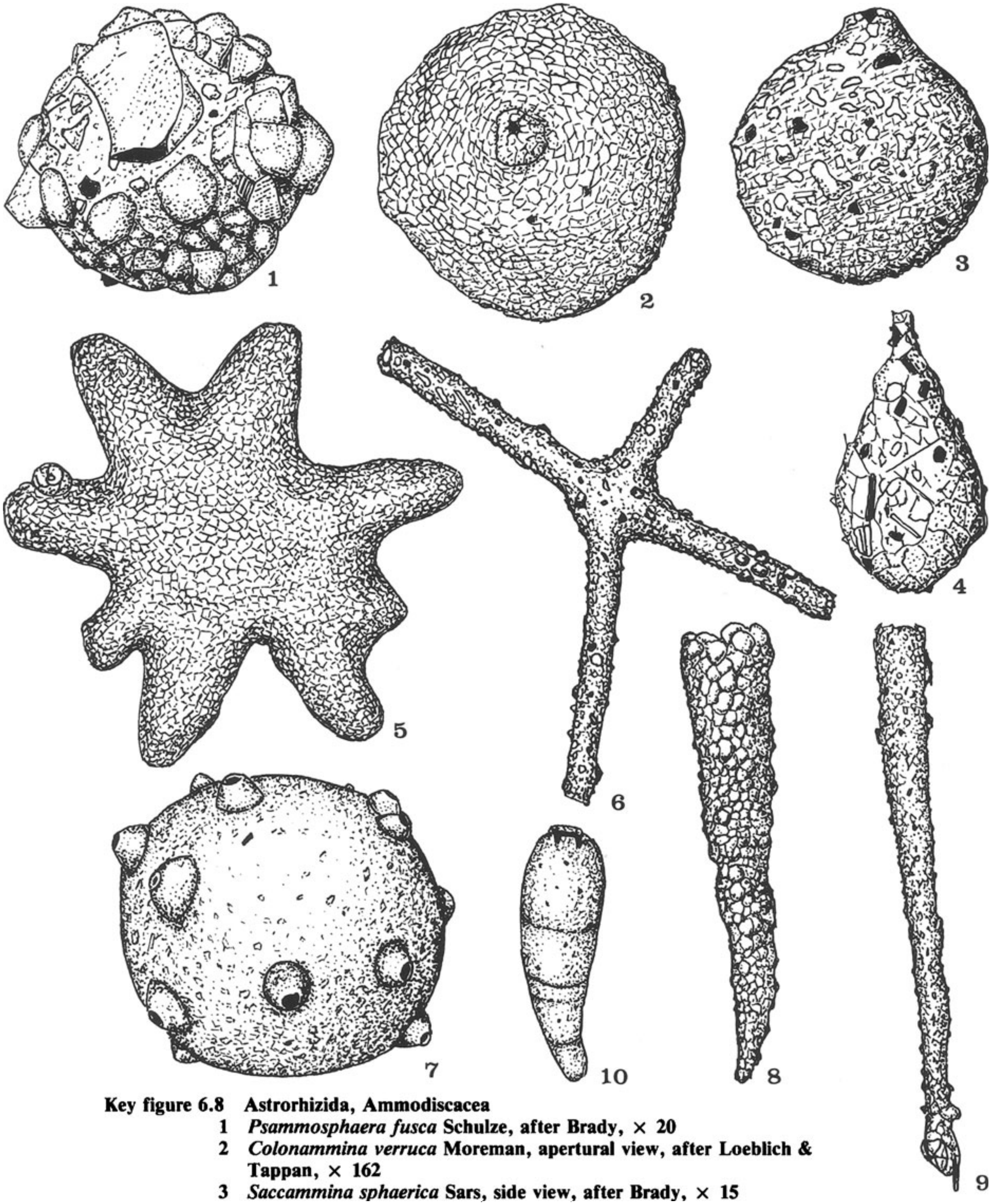
MAIN FAMILIES AND IMPORTANT GENERA OF AGGLUTINATING FORAMINIFERA

ASTRORHIZIDA	non-septate; Camb. – Rec.
AMMODISCACEA	subspherical or tubular, straight, branched or enrolled and sometimes with initial end swollen or constricted as proloculus; Camb. – Rec. Key figures 6.8 and 6.9.
SACCAMMINIDAE	subspherical; Ord. – Rec. Key figure 6.8.
Psammosphaera (no. 1)	free without definite aperture; ?Camb. – Rec. (pseudocolony = *Sorosphaera).*
Colonammina (no. 2)	attached, hemispherical, aperture produced at summit; Sil. – Rec. (pseudocolony = *Ammopemphix,* aperture at periphery = *Tholosina*).
Saccammina (no. 3)	globular, aperture round, produced; Sil. – Rec.
Lagenammina (no. 4)	flask shaped; Sil. – Rec.
Thurammina (no. 7)	aperture multiple, produced; Sil. – Rec.
ASTRORHIZIDAE	tubular or branching; Camb. – Rec. Key figure 6.8
Astrorhiza (no. 5)	substellate and flattened, many arms; Ord. – Rec. (globular with few arms = *Astrammina,* Quat.).
Rhabdammina (no. 6)	three to five arms radiating from small central cavity; Ord. – Rec. (two opposite arms = *Oculosiphon,* Rec.).
Jacullela (nos. 8/9)	elongate conical, aperture at larger end; Jur. – Rec.
Hippocrepina (no. 10)	conical, rounded oval end, aperture small, growth constrictions; Dev. – Rec.
Hyperammina (no. 11)	initial end bulbous, narrowing to aperture; Ord. – Rec. (pseudolabyrinthic spicular interior = *Botellina,* ?Quat.).
Saccorhiza (no. 12)	initial end bulbous, narrowing to dichotomously branching tube, partly spicular; Carb. – Rec.
Dendrophyra (no. 13)	attached, arborescent; Quat.
Halyphysema (no. 14)	attached, clavate, may branch at summit, partly spicular; Quat. (cylindrical, spicular throughout = *Technitella*).
Rhizammina (no. 15)	flexible branching tube, loosely agglutinating with dead foram. shells; Quat.

Bathysiphon (nos. 16/17)	slightly flaring or straight-sided tube, spicular, may have growth constrictions; ?Cret. – Rec. (closed at one end = *Protobotellina,* Quat.; finely arenaceous with transverse layering = *Platysolenites,* L. Camb., ? = *Psammosiphonella*, Ord. – Rec; argillaceous = *Argillotuba,* Rec.; micaceous = *Micatuba,* Rec.).
AMMODISCIDAE	enrolled tubular to unwound; Sil. – Rec. Key figure 6.9.
Glomospira (nos. 1/2)	irregularly winding; Sil. – Rec.
Glomospirella (no. 3)	final whorls planispiral; Sil. – Rec.
Ammodiscus (nos. 4/5)	planispiral throughout; Sil. – Rec.
Turritellella (no. 6)	elongate trochospire; Sil. – Rec.
Lituotuba (no. 7)	irregularly winding then uncoiled; Sil. – Rec.
Tolypammina (no. 8)	attached, irregularly uncoiled; Sil. – Rec.
Ammolagena (no. 9)	attached, globular then narrowly tubular, probably parasitic; Sil. – Rec.
LITUOLIDA	multilocular; Carb. – Rec.
LITUOLACEA	planispiral to biserial and uniserial; Carb. – Rec. Key figures 6.9 and 6.10.
LITUOLIDAE	planispiral to uncoiled uniserial or annular; Carb. – Rec. Key figure 6.9.
Trochamminoides (no. 10)	planispiral, evolute, chambers irregular length; Carb. – Rec.
Haplophragmoides (nos. 11/12)	planispiral, involute; Carb. – Rec. (areal apertures = *Cribrostomoides*).
Ammotium (no. 13)	lenticular, final chambers tending to uncoil, high, aperture terminal; Cret. – Rec.
Ammobaculites (no. 14)	final chambers uncoiled, short, round; Carb. – Rec. (streptospiral initial part and labyrinthic = *Haplophragmium* (Emend. Lindenberg 1967); multiple aperture = *Lituola;* labyrinthic also = *Pseudocyclammina,* U. Jur. – U. Cret.).
Reophax (no. 15)	uniserial, round in section; Dev. – Rec. (globular chambers = *Hormosina*).
Ammomarginulina (nos. 16/17)	final chambers short, compressed; Carb. – Rec.
Flabellammina (nos. 21/22)	final chambers chevron shaped; Jur. – Cret. (labyrinthic = *Flabellamminopsis*).
Triplasia (nos. 24/25)	final chambers trigonal or quadrangular, labyrinthic; Jur. – Rec.
Cyclammina (nos. 18 – 20)	planispiral, involute, intricately labyrinthic, apertures areal; Cenozoic (simple alveolar wall = *Alveophragmium*). Allied Cretaceous genera include *Loftusia,* fusiform; *Choffatella,* compressed with apertures in vertical row; *Feurtillia,* final chambers uncoiled with vertical apertural slit. (See figure 6.2 for ranges.)
Ammocycloloculina (no. 23)	discoid, final chambers annular, apertures peripheral; Cret. (2 layers with radial partitions = *Dicyclina*).

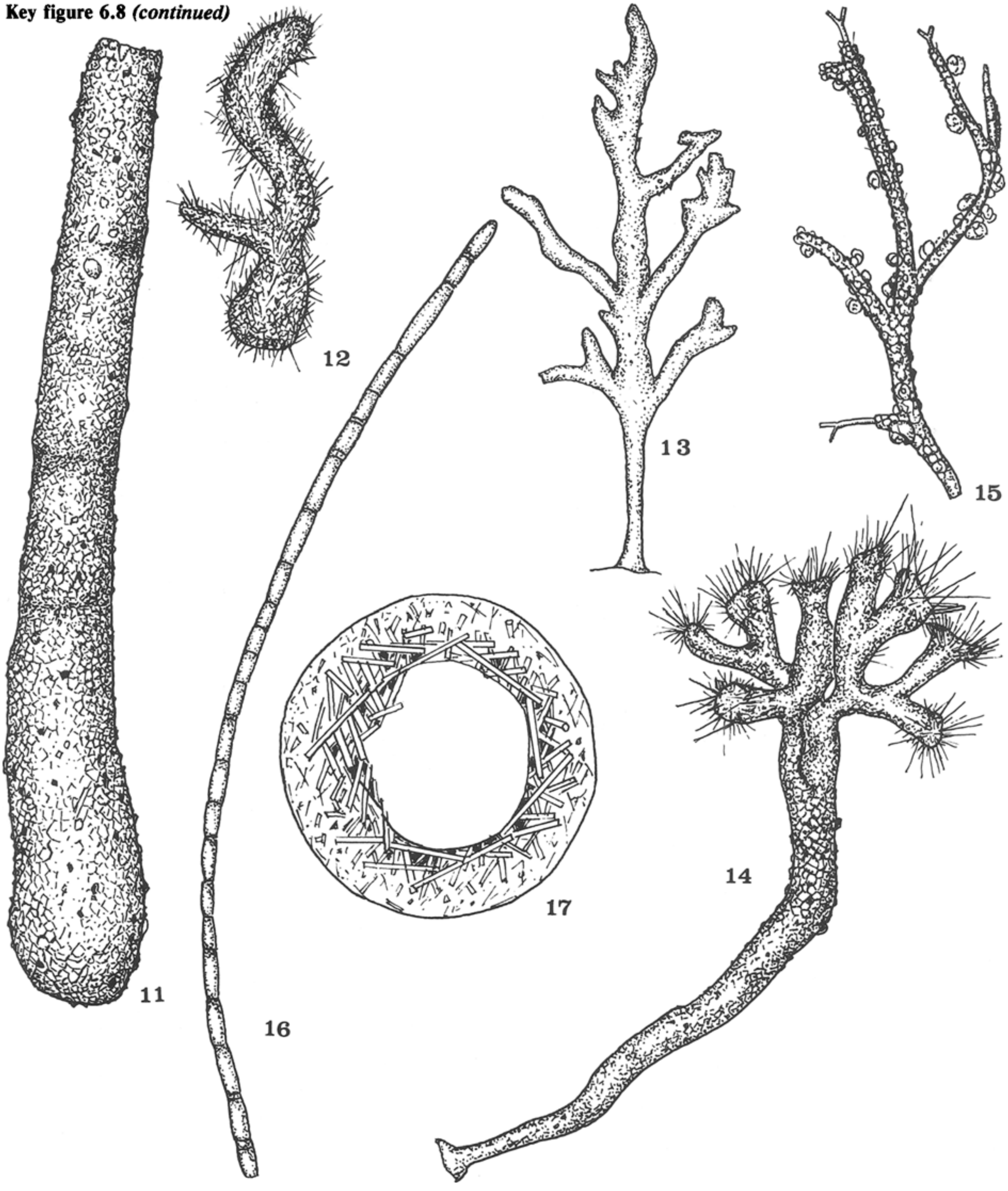
TEXTULARIIDAE	planispiral to biserial and uniserial, aperture basal to terminal; Cret. – Rec. Key figure 6.10.
Spiroplectammina (nos. 1/2)	final chambers biserial; Cret. – Rec.
Textularia (nos. 3/4)	biserial throughout; Cret. – Rec. (internal pillars = *Tawitawia,* Quat.).
Bigenerina (no. 5)	final chambers uniserial, round, aperture terminal; Cret. – Rec.
Vulvulina (nos. 6/7)	final chambers uniserial, compressed, aperture a terminal slit; Cret. – Rec.
ATAXOPHRAGMIACEA (*nom. transl.* Grigelis 1978a)	multilocular, trochospiral; Carb. – Rec. Key figures 6.10 and 6.11.
TROCHAMMINIDAE	low trochospiral, aperture basal, areal or peripheral; Carb. – Rec. Key figure 6.10.
Trochammina (nos. 8 – 10)	aperture ventral basal; Carb. – Rec. (radial and transverse partitions = *Dictyopsella,* U. Cret.).
Jadammina (no. 11)	very low trochospiral, areal apertures in addition to basal one; Quat. (areal apertures only = *Entzia*).
Arenoparrella (no. 12)	aperture a peripheral slit; Neogene.
Tritaxis (no. 13)	attached, chambers overlapping, aperture areal at suture; Quat. (few, high, inflated chambers = *Cystammina*).
Tiphotrocha (no. 14)	aperture umbilical, beneath a lobe; Neogene.
VERNEUILINIDAE	high trochospiral to uniserial, aperture basal to terminal, and multiple; Trias. – Rec. Key figure 6.10.
Verneuilina (nos. 15/16)	triserial; Trias. – Rec. (multiple terminal aperture and vertical partitions = *Hensonia,* U. Cret.).
Dorothia (nos. 17/18)	multiserial to biserial; Cret. – Rec. (buttresses giving pseudolabyrinthic structure = *Textulariella,* Cen.; vertical and horizontal partitions = *Pseudotextulariella,* U. Cret.).
Tritaxia (nos. 19/20)	triserial to uniserial, aperture terminal with internal tube; Cret. – Rec.
Gaudryina (nos. 21/22)	triserial to biserial; Trias. – Rec.
Spiroplectinata (no. 23)	triserial to biserial and uniserial, aperture produced; Cret.
Cribrogoesella (no. 24)	multiserial to biserial and uniserial, aperture multiple; Neogene.
VALVULINIDAE	trochospiral to uniserial, aperture umbilical to terminal, valvular tooth; Mes. – Rec. Key figure 6.11.
Valvulammina (nos. 1/2)	low trochospiral; Cret. – Rec.
Valvulina (nos. 3/4)	high trochospiral, triserial; ?U. Trias. – Rec.
Clavulina (nos. 5/6)	triserial to uniserial, aperture terminal; Cenozoic (triangular = *Clavulinoides;* uniserial = *Dusenburyina,* Quat.).
Cribrobulimina (no. 7)	becomes loosely spiral, apertures around tooth; Quat.
EGGERELLIDAE	trochospiral to uniserial, aperture basal areal to multiple terminal; Cenozoic. Key figure 6.11.

Plectotrochammina (nos. 8/9)	final few chambers biserial; Cenozoic.
Eggerella (no. 10)	final chambers triserial; Cenozoic.
Karreriella (no. 11)	well developed, twisted biserial stage, apertural lip or neck; M. Tert. – Rec.
Multifidella (nos. 12/13)	well-developed uniserial stage, apertures terminal slits with lips; Neogene.
ATAXOPHRAGMIIDAE	trochospiral to biserial/uniserial or loosely spiral, aperture high arch or loop shaped to terminal; Jur. – Rec. Key figure 6.11.
Arenobulimina (no. 14)	later chambers loosely spiral; Cret. – Eoc. (thickened central core = *Pfenderina,* Jur. – Cret.; vertical partitions = *Ataxophragmium,* Cret.; core with marginal vertical partitions and becoming uniserial = *Kornubia,* Jur. – Cret.).
Eggerellina (nos. 15/16)	triserial, globular; Cret. (internal toothplate = *Eggerelloides,* ? Neogene).
Migros (nos. 17/18)	triserial to biserial; Jur. – Rec.
Pseudobolivina (no. 19)	biserial to uniserial; Jur. – Rec.
ORBITOLINIDAE	asymmetric trochospiral to uniserial conical, multiple apertures with internal buttresses and/or partitions; Jur. – Palaeogene. Key figure 6.11.
Lituonella (nos. 20/21)	later chambers uniserial with buttresses, Palaeogene (buttresses rudimentary = *Pseudolituonella,* Cret.; restricted to central zone = *Kilianina,* Jur. – Cret.).
Coskinolina (nos. 22/23)	adult conical, with buttresses and marginal radial partitions; Cret. – Eocene (horizontal partitions also = *Dictyoconus*).
Coskinoloides (nos. 24/25)	radial partitions partially extending to chamber centre; Cret.
Orbitolina (nos. 26 – 28)	zig-zag radial partitions in central zone, one or more series of marginal vertical and horizontal plates; Cret.

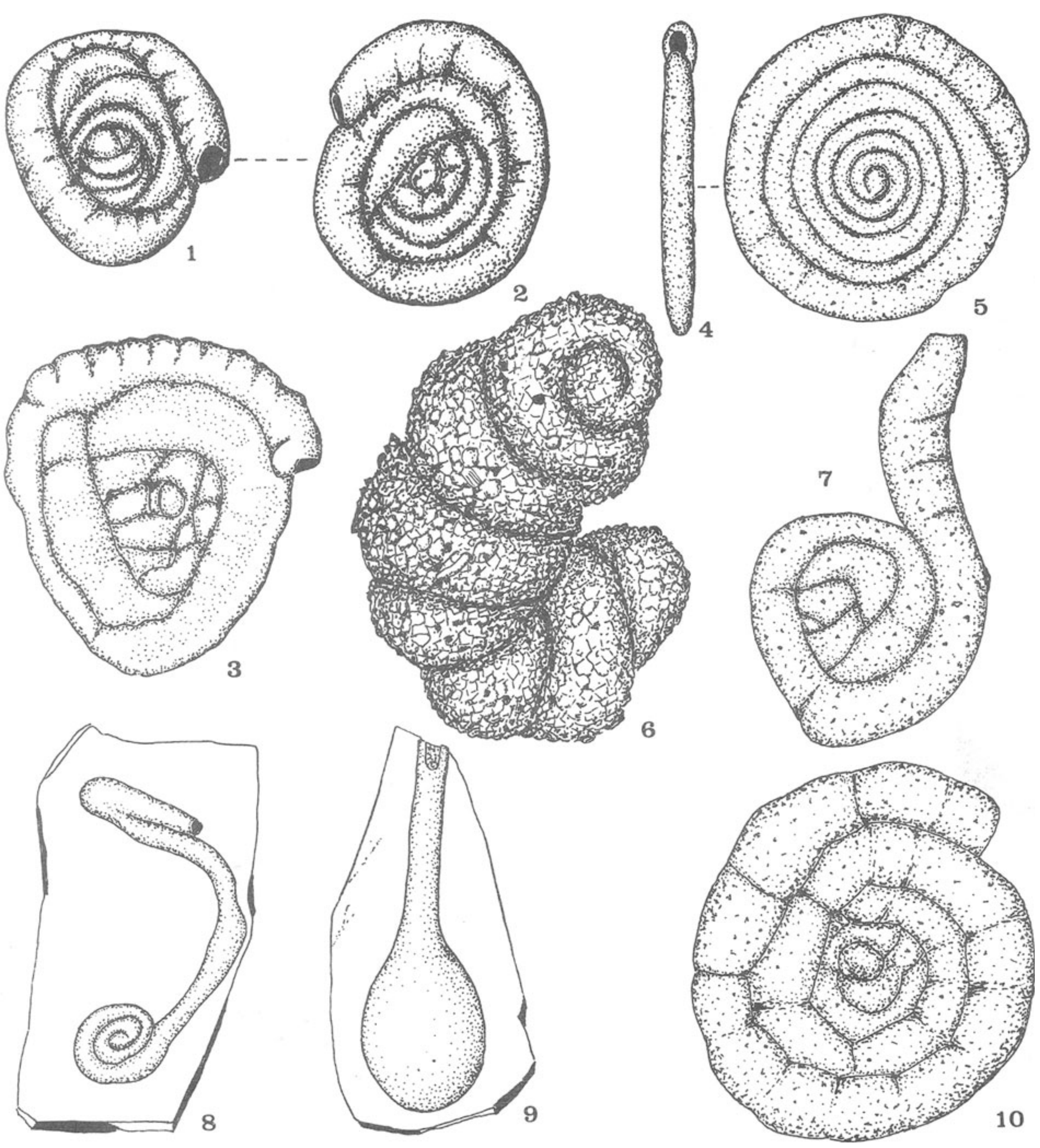


Key figure 6.8 **Astrorhizida, Ammodiscacea**
1 ***Psammosphaera fusca*** **Schulze, after Brady, × 20**
2 ***Colonammina verruca*** **Moreman, apertural view, after Loeblich & Tappan, × 162**
3 ***Saccammina sphaerica*** **Sars, side view, after Brady, × 15**
4 ***Lagenammina ampullacea*** **(Brady), side view, × 50**
5 ***Astrorhiza arenaria*** **Norman, dorsal view, after Brady, × 8**
6 ***Rhabdammina abyssorum*** **Sars, dorsal view, after Brady, × 10**
7 ***Thurammina papillata*** **Brady, side view, × 48**
8/9 ***Jaculella acuta/obtusa*** **Brady, side views, × 15**
10 ***Hippocrepina indivisa*** **Parker, side view, after Brady, × 45**

Key figure 6.8 ***(continued)***



11 *Hyperammina elongata* **Brady, side view, × 10**
12 *Saccorhiza ramosa* **(Brady), side view, × 10**
13 *Dendrophyra erecta* **Strethill-Wright, side view, after Brady, × 30**
14 *Halyphysema ramulosa* **Bowerbank, side view, after Brady, × 20**
15 *Rhizammina algaeformis* **Brady, side view, × 8**
16/17 *Bathysiphon filiforme* **Sars, side view and horizontal section after Brady, × 3 and × 60**



Key figure 6.9 Astrorhizida, Lituolida, Ammodiscacea, Lituolacea

1/2 *Glomospira gordialis* **(Jones & Parker), side views, after Brady, × 140**

3 *Glomospirella umbilicata* **(Cushman & Waters), side view, after Loeblich & Tappan, × 68**

4/5 *Ammodiscus tenuis* **Höglund, peripheral and side views, after Brady, × 15**

6 *Turritellella spectabilis* **(Brady), side view, × 12**

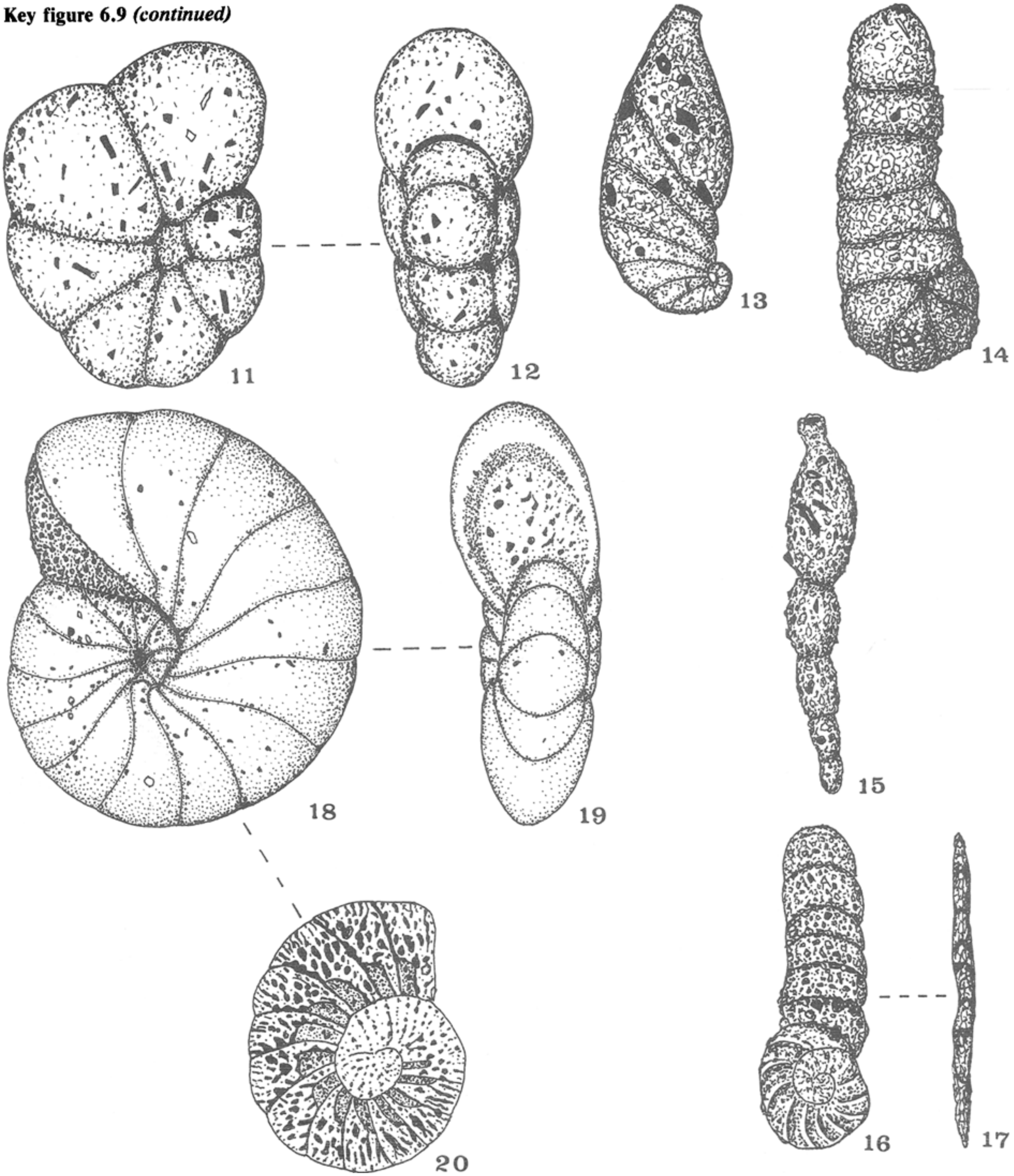
7 *Lituotuba lituiformis* **(Brady), side view, × 40**

8 *Tolypammina vagans* **(Brady), dorsal view, × 100**

9 *Ammolagena clavata* **(Jones & Parker), dorsal view, after Brady, × 25**

10 *Trochamminoides proteus* **(Karrer), side view, after Brady, × 50**

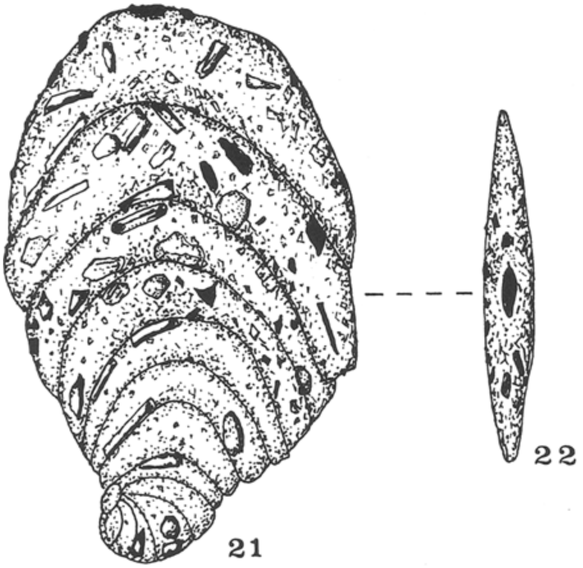
Key figure 6.9 ***(continued)***

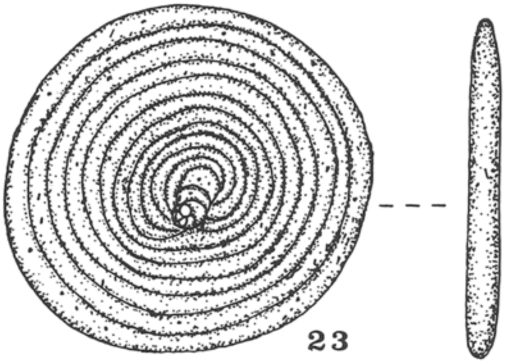


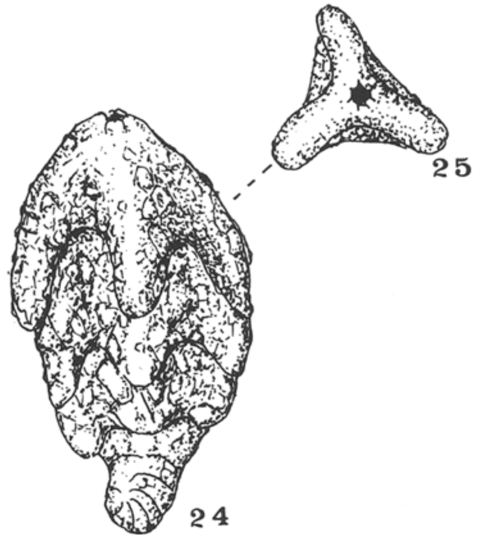
11/12 *Haplophragmoides canariense* (d'Orbigny), side and peripheral views, after Cushman, × 60
13 *Ammotium cassis* (Parker), side view, after Brady, × 35
14 *Ammobaculites calcareus* (Brady), side view, × 18
15 *Reophax dentaliniformis* Brady, side view, × 40
16/17 *Ammomarginulina foliaceus* (Brady), side and peripheral views, × 25
18 – 20 *Cyclammina cancellata* Brady, side and peripheral views, and vertical section, × 15

(continued overleaf)

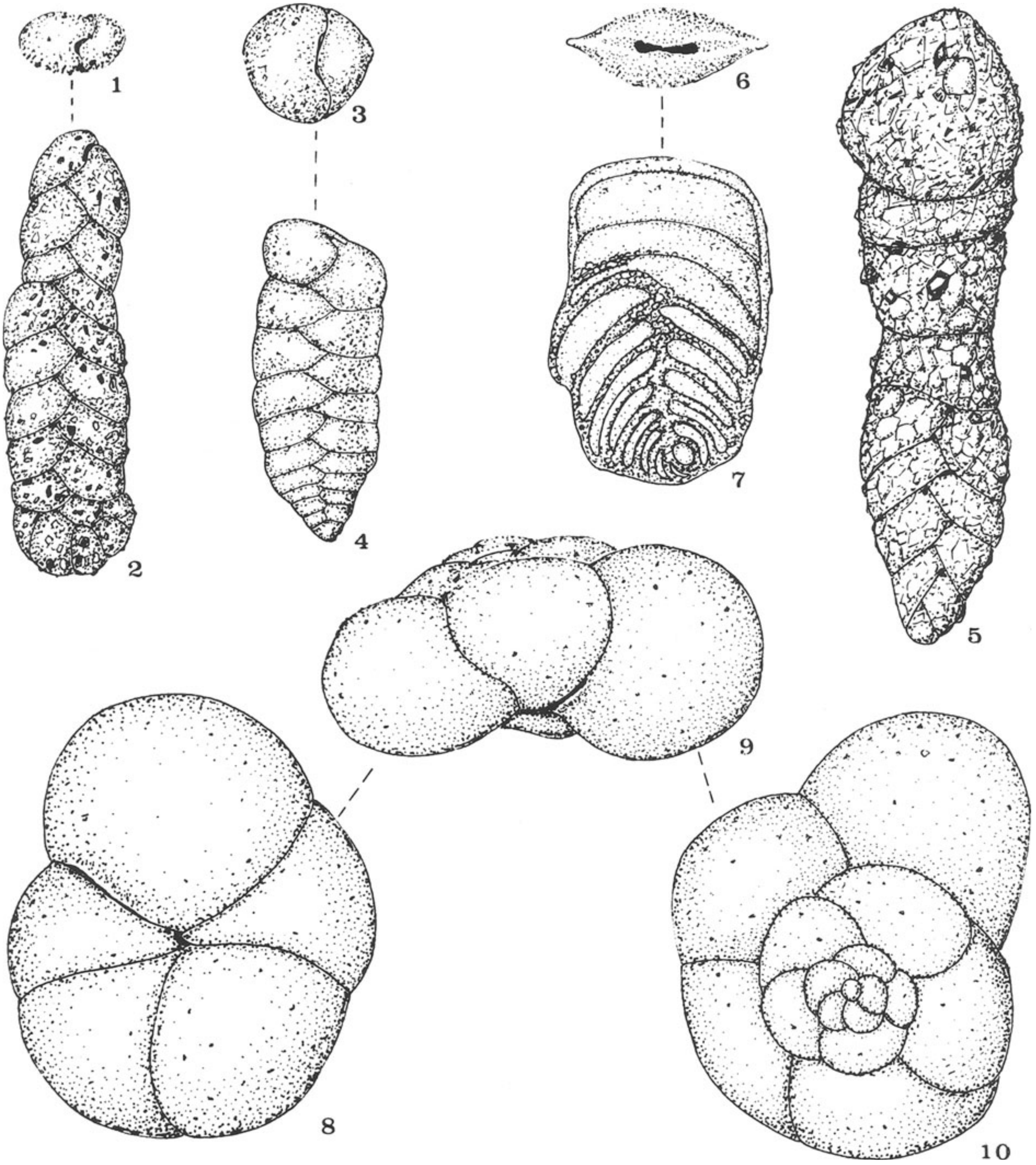
Key figure 6.9 ***(continued)***







21/22 ***Flabellammina alexanderi*** **Cushman, side and apertural views, after Loeblich & Tappan, × 32**
23 ***Ammocycloloculina erratica*** **(Joukowsky & Faure), side and peripheral views, × 10**
24/25 ***Triplasia goodlandensis*** **(Cushman & Alexander), side and apertural views, after Loeblich & Tappan, × 55**



Key figure 6.10 **Lituolida, Lituolacea, Ataxophragmiacea**

1/2 ***Spiroplectammina biformis*** **(Parker & Jones), side and apertural views, after Loeblich & Tappan, × 100**

3/4 ***Textularia sagittula*** **Defrance, side and apertural views, after Loeblich & Tappan, × 26**

5 ***Bigenerina nodosaria*** **d'Orbigny, side view, after Brady, × 70**

6/7 ***Vulvulina pennatula*** **(Batsch), side and apertural views, after Loeblich & Tappan, × 40**

8–10 ***Trochammina inflata*** **(Montagu), ventral, peripheral and dorsal views, after Brady, × 100**

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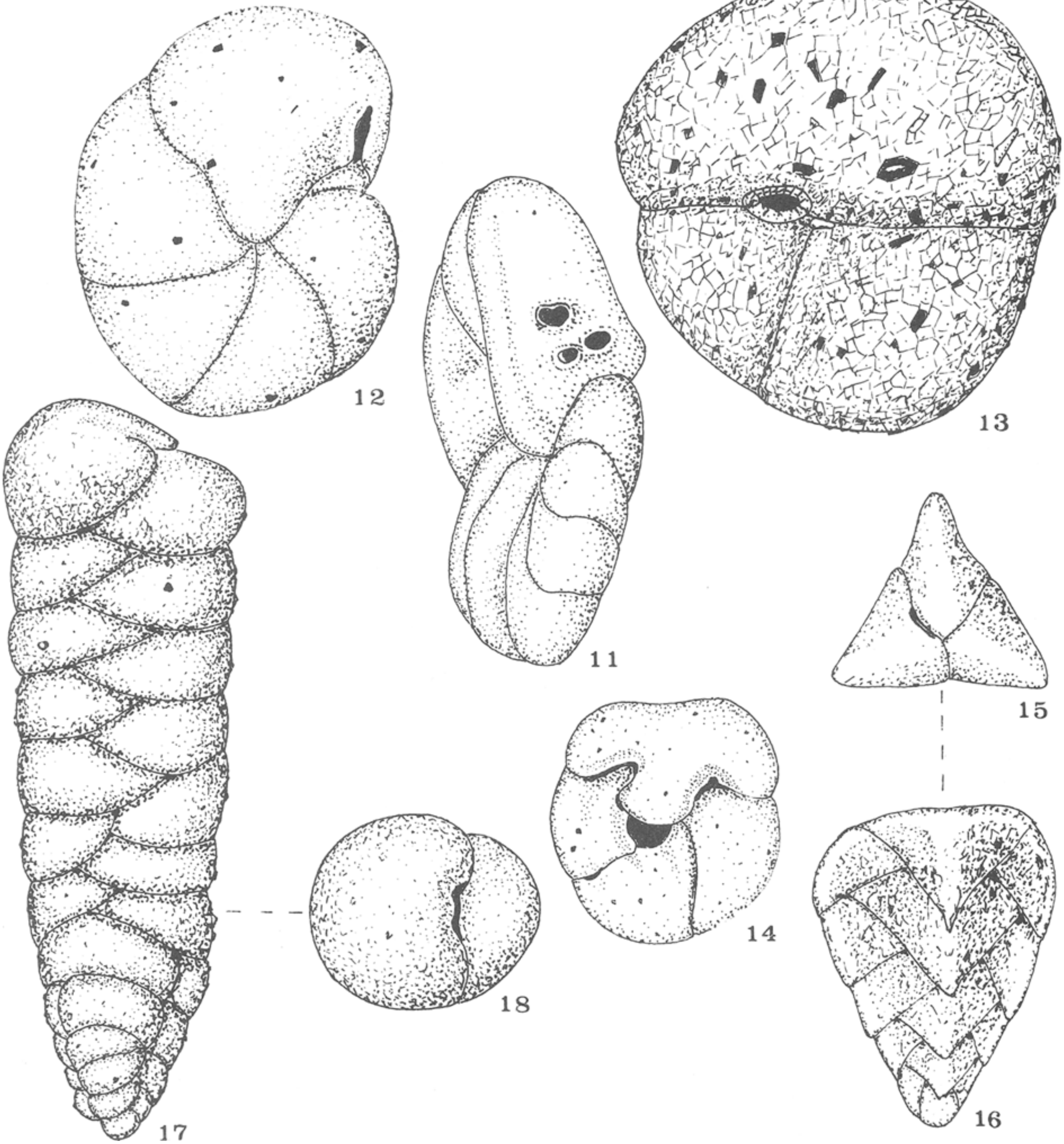
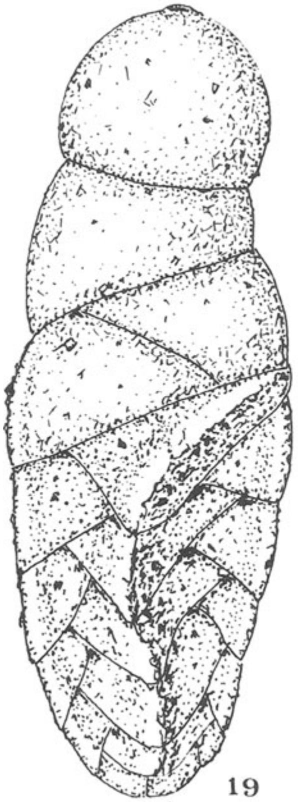
Key figure 6.10 ***(continued)***



11 *Jadammina macrescens* **(Brady), peripheral view, after Loeblich & Tappan, × 200**
12 *Arenoparrella mexicana* **(Kornfeld), ventral view, after Loeblich & Tappan, × 218**
13 *Tritaxis fusca* **(Williamson), ventral view, after Loeblich & Tappan, × 100**
14 *Tiphotrocha comprimata* **(Cushman & Brönniman), ventral view, after Loeblich and Tappan, × 70**
15/16 *Verneuilina tricarinata* **d'Orbigny, apertural and side views, × 15**
17/18 *Dorothia bradyana* **Cushman, side and apertural views, after Brady, × 40**

Key figure 6.10 ***(continued)***



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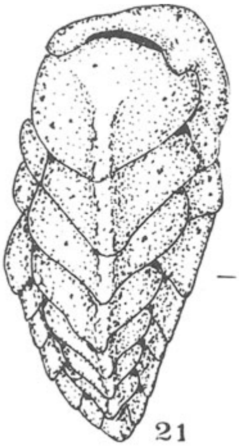

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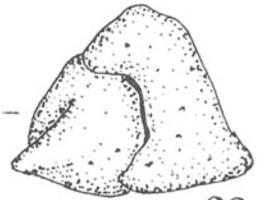

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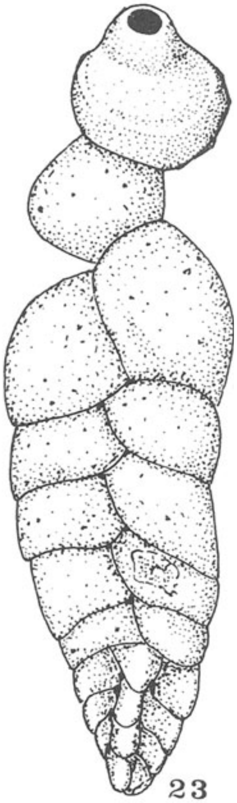

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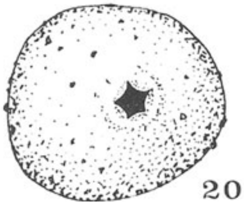

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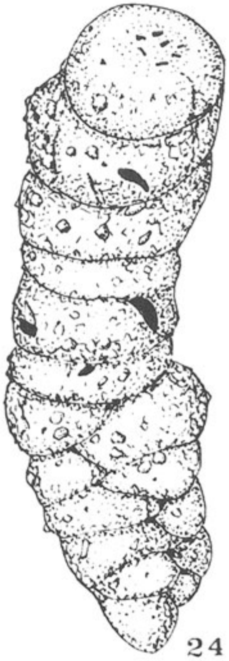

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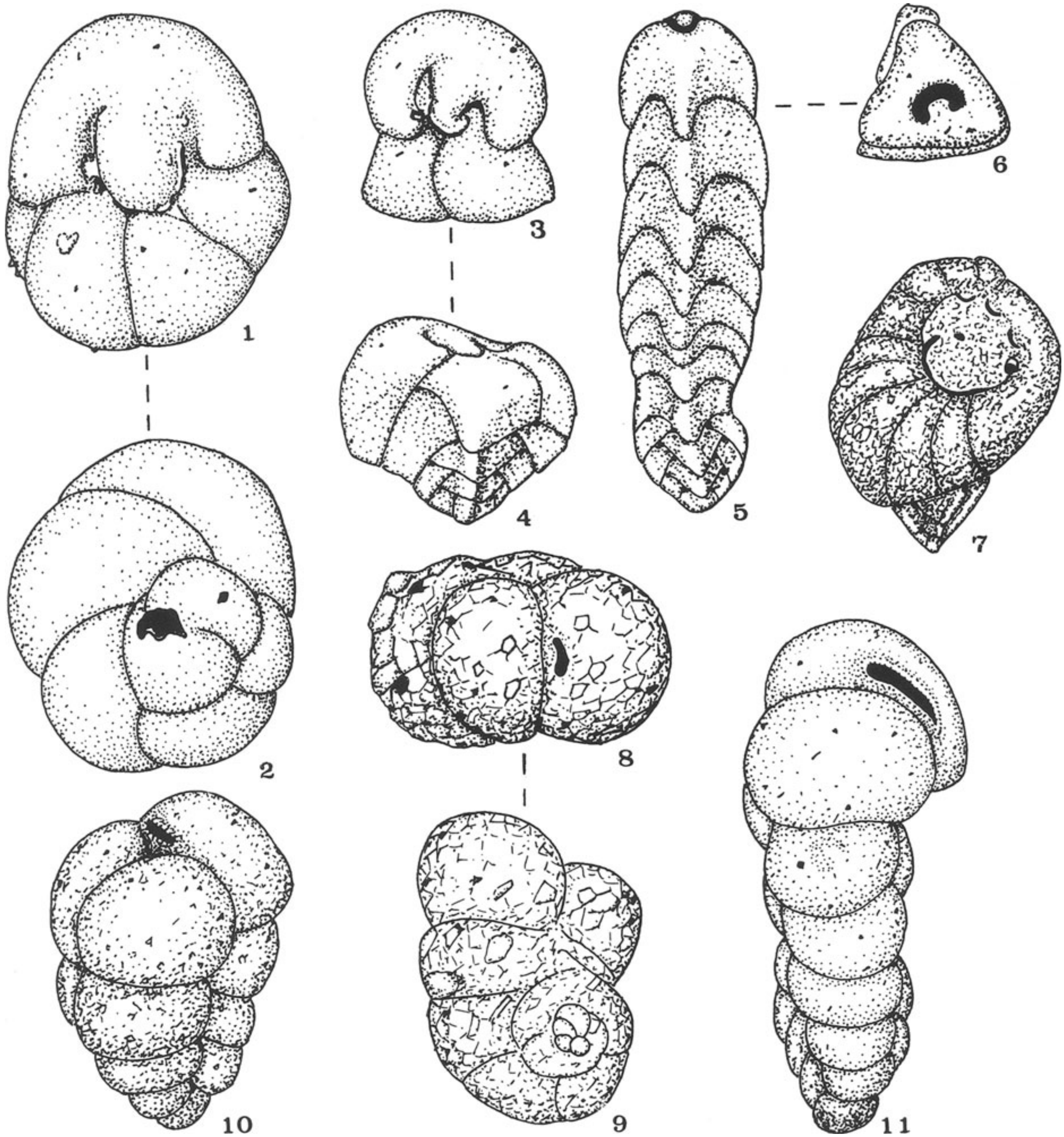
19/20 *Tritaxia capitosa* **(Cushman), side and apertural views, after Loeblich & Tappan, × 62**

21/22 *Gaudryina atlantica* **Bailey, side and apertural views, after Brady, × 14**

23 *Spiroplectinata annectens* **(Parker & Jones), side view, after Loeblich & Tappan, × 74**

24 *Cribrogoesella robusta* **(Brady), side view, after Loeblich & Tappan, × 17**



Key figure 6.11 **Lituolida, Ataxophragmiacea**

1/2 *Valvulammina globularis* **(d'Orbigny), ventral and dorsal views, after Loeblich & Tappan, × 50**

3/4 *Valvulina triangularis* **d'Orbigny, apertural and side view, after Loeblich & Tappan, × 33**

5/6 *Clavulina angularis* **d'Orbigny, side and apertural views, × 48**

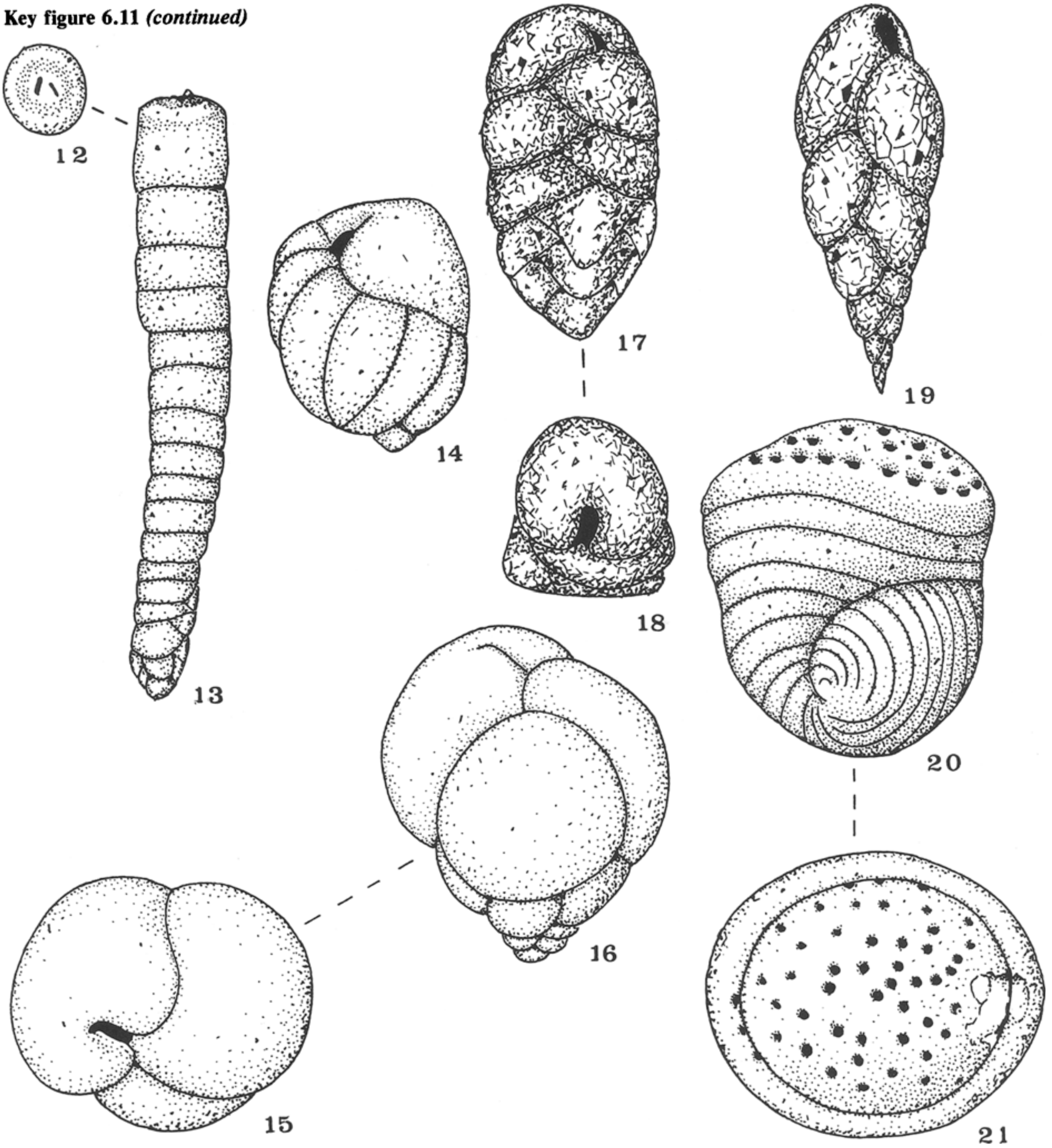
7 *Cribrobulimina mixta* **Cushman, oblique apertural view, after Loeblich & Tappan, × 45**

8/9 *Plectotrochammina subglobosa* **Parr, apertural and side views, after Loeblich & Tappan, × 50**

10 *Eggerella bradyi* **(Cushman), side view, after Loeblich & Tappan, × 65**

11 *Karreriella novangliae* **(Cushman), side view, after Brady, × 40**

Key figure 6.11 ***(continued)***



12/13 ***Multifidella nodulosa*** **(Cushman), apertural and side views, after Loeblich & Tappan, × 20**
14 ***Arenobulimina presli*** **(Reuss), side view, after Loeblich & Tappan, × 100**
15/16 ***Eggerellina brevis*** **(d'Orbigny), apertural and side views, after Loeblich & Tappan, × 64**
17/18 ***Migros medwayensis*** **(Parr), side and apertural views, after Loeblich & Tappan, × 36**
19 ***Pseudobolivina antarctica*** **Heron-Allen & Earland, side view, × 90**
20/21 ***Lituonella roberti*** **Schlumberger & Schlumberger, side and apertural views, after Loeblich & Tappan, × 17**

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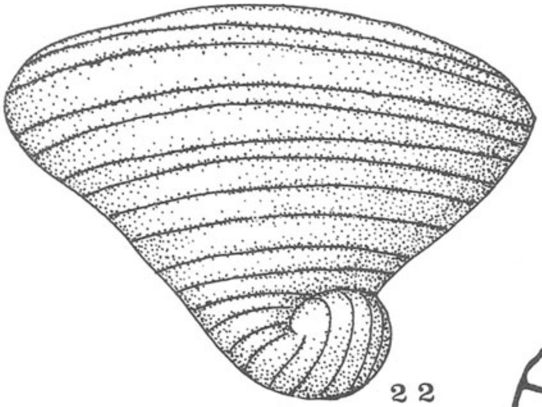
Key figure 6.11 *(continued)*



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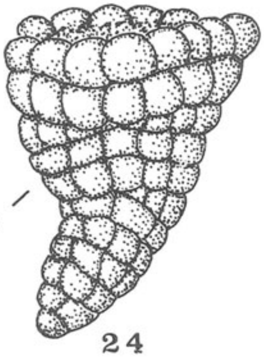

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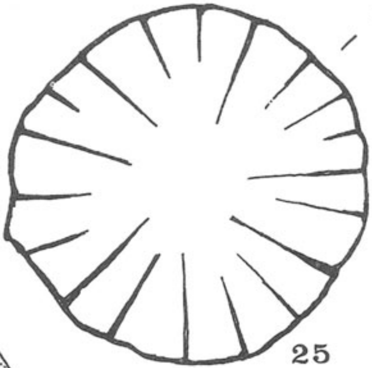

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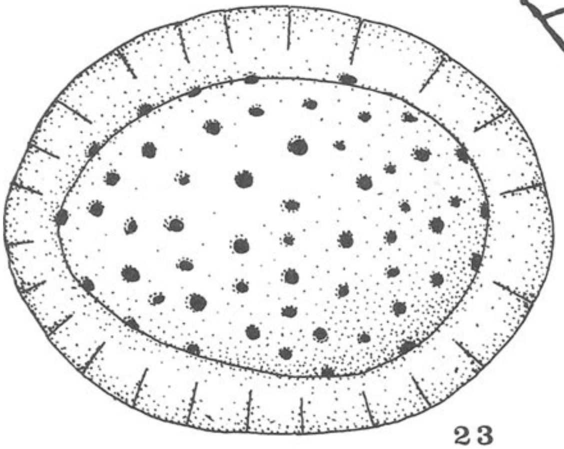

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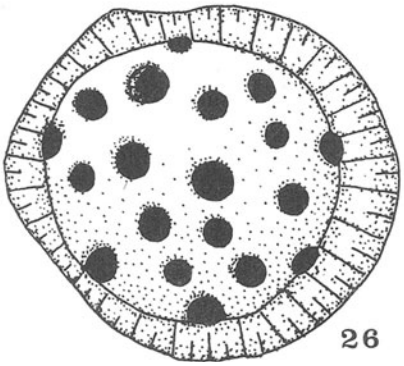

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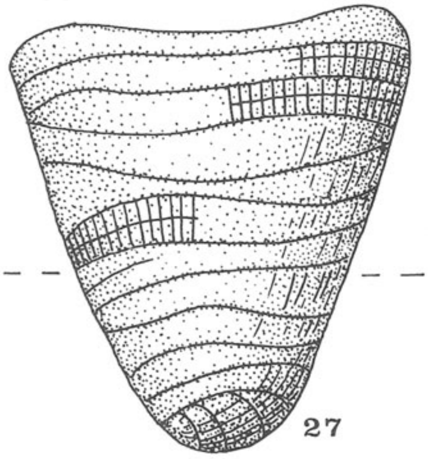

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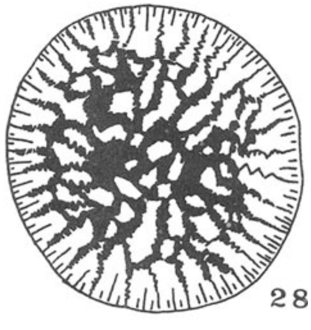

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22/23 *Coskinolina liburnica* **Stache, side and apertural views, after Schubert, × 17**

24/25 *Coskinoloides texanus* **Keijzer, side views and horizontal section, after Loeblich & Tappan, × 100 and × 66**

26–28 *Orbitolina mosae* **(Hofker), apertural and side views and horizontal section, × 66**

Chapter 7

The Fusulinida

> ... secondary alteration, during the diagenesis of the host sediment, has had a marked effect on the mode of preservation of Palaeozoic foraminiferal assemblages. In particular, such alteration may lead to changes in composition and texture of the test wall, distortion of form by leaching and crushing, and reduction in faunal content. The main processes of alteration include redistribution and recrystallisation, dolomitisation, silicification and compaction.
>
> (Cummings, 1955)

Agglutinated Foraminifera remained the dominant group in the Lower Palaeozoic but a spectacular increase in number and kinds of Foraminifera occurred in the Upper Palaeozoic with the rise of the calcareous microgranular group. With the advent of wholly secreted tests, Foraminifera became important contributors to limestones, especially the 'robust' fusulinaceans which were the first to evolve complex architecture combined with relatively giant size. As pointed out by Thompson (1964) well-preserved fusulinaceans, alone, far outnumber any other single invertebrate group in the Upper Carboniferous and Permian of many areas. In some cases they exceed in number and volume the combined remains of all other groups. Foraminifera now provide valuable stratigraphical index fossils, and inter-regional correlation is possible on the basis of worldwide zones.

The difficulties faced by earlier workers in deciding the original wall structure in this group have been noted in chapter 4. This debate has been decided largely in favour of the idea that the wall is built of directly secreted granules without optical alignment but generally in layers (Henbest, 1937; Wood, 1949a; Reitlinger, 1950; Cummings, 1956), although doubt remains. This is because of the inevitable alteration and recrystallisation of a high proportion of calcareous tests in rocks over 250 million years old. A number of early workers, such as Cushman, were inclined to regard the group as agglutinated because, after treatment with dilute HCl, many species leave a residue of quartz particles. However, Cummings (1955), after a study of diagenesis in the Lower Carboniferous, discovered that this 'acid test' is inadequate and misleading. For instance, in the case of assemblages from the limestones of Law Quarry, Ayrshire, Scotland, quartz particles are not found in residues of unaltered specimens, only in the case of silicified ones. Again, Henbest (1963) found secondary enlargement of quartz crystals common in the Pennsylvanian of Arkansas but found discrete quartz crystals only when hydrothermal metamorphism was evident in the matrix.

Variable silicification is a feature of many localities in the British Avonian. Thus in the *Michelinia* Zone of Northern England, beekitisation affects brachiopods and corals but leaves the Foraminifera unaffected, while in the Yoredales and Lower Limestones of Scotland there is often complete silicification of the fauna. A further difficulty is that many species clearly do incorporate extra adventitious material into a basically secreted wall.

Cummings' work (1955, 1956) also shows that although dolomitisation, with replacement of the original calcite structures without destruction, occurs rarely, growth of dolomite rhombs is usually at the expense of the test. Iron replacement is also common and in the case of the microfauna of the Wilkieston Quarry, Fife, Scotland, the calcite granules are replaced by ferrodolomite with varying proportions of limonite, itself a replacement product after siderite; this results in a roughened test, extremely dark and almost opaque in thin section.

Recrystallisation of layered test walls with randomly arranged granules in the outer layer, as in palaeotextulariids, often leads to formation of isolated and irregularly shaped particles of larger grain size, of calcite or allied secondary minerals. These may be scattered irregularly through the wall, or stand out on weathered surfaces of the test, in which case the test may be misinterpreted as agglutinated. Recrystallisation of the regularly arranged (stacked) granules of the 'fibrous' layer gives an irregular mosaic of clear calcite, often indistinguishable from the matrix. In this case a basically two-layered test may be thought to consist of one layer only.

These processes of alteration may explain the apparent differences in structure recorded in members of the Endothyridae, some being described as exhibiting homogeneous, microgranular walls. Because recrystallisation usually involves increase in grain size, Wood (1949a) was satisfied that the granular wall of *Endothyra* was not a recrystallised radial wall. But he did not rule out the possibility that it might represent a recrystallised, minutely crystalline wall, similar to that in the porcelaneous genus, *Alveolinella*. However, he concluded that the advanced fusulines were all built on basically the same plan and were minutely granular. The durability of very fine details and the moderate transparency of the wall in *Fusulina, Triticites* and *Schwagerina* is considered to indicate the stability of the shell structure in this group (Henbest, 1963). On the other hand, Henbest also noted that the endothyrids are generally as dark as the tectum of the fusulines and so may be different in composition. As both endothyrids and tournayellids are generally as dark as the matrix, Skipp *et al.* (1966) suggest that most examples are recrystallised. They cite the case of *Septatournayella henbesti* in which small portions of the test appear to be translucent, microcrystalline and finely perforate and grade into the typical, dark microgranular material. In support of the idea that the wall in *Endothyra* is generally recrystallised, Loeblich and Tappan (1964) and Brenckle (1973) have distinguished two or even three layers in well-preserved material. In *Endothyra bowmani,* Loeblich and Tappan distinguish a dark, outer 'tectum', from a lighter, inner 'diaphanotheca' of clear calcite. The inner layer is described as 'fibrous', so is presumably of stacked granules, as in the palaeotextulariids. The third layer reported may be the same as the inner lining or 'tectorium' of the higher fusulines (see below and figure 4.4D).

Another 'disconcerting fact' noticed by a number of workers (Henbest, 1963; Thompson, 1964) is that members of the Ozawainellidae and Staffellidae (Ozawainellidae herein) are invariably replaced by clear, coarsely crystalline calcite, although other fusulinids in the same associations are unaltered. This prompted Henbest to suggest that the original composition in these families may even have been aragonitic. Thus, although the evidence in support of an original microgranular structure is reasonably secure for the palaeotextulariids and the higher fusulines, it is less so for some other groups. Families in which there is optical alignment (described as vitreous), as in the Archaediscidae, should be separated as a distinct suborder if not excluded altogether (see the Summary Classification at the end of the chapter).

Difficulties in classification are caused not only by alteration but by the distortion and damage caused by compaction. As might be expected this is most frequent in argillaceous sediments. It can lead to serious misinterpretation, as in the case of *Climacammina* in which the initial biserial part was considered trochoid by Brady (1876) on the basis of what turned out to be a crushed specimen. Great care must also be taken in interpretation of specimens seen only in thin sections of limestones. Firm determinations should never be made on the basis of imperfect or oblique sections alone. The confusion that can arise was well shown by Sosnina (1960), who was able to prove that several new genera had been set up in error on random sections of *Pachyphloia*. However, as pointed out by Cummings (1956, 1958), the identity of a specimen in a good thin section can often 'be established by detailed morphologic comparison with the sequence and character, of the known ontogenetic stages of the various genera'.

The student should be forewarned by the discovery that a number of genera ascribed by earlier workers to this group on the basis of inadequate material, often represented only by random sections and too often with no evidence of apertures, are not Foraminifera at all (Loeblich and Tappan, 1974). Thus *Umbellina* and its allies appear to be charophytes (Miklukho-Maklay, 1961) and similarly *Stacheia* and its allies are removed from the attached family Ptychocladiidae and grouped with the red algae (Mamet and Rudloff, 1972). In addition, Kazmierczak (1976) claims that most Palaeozoic calcispheres and certain supposed parathuramminids are actually volvocaceans. Others may be radiolarians or testaceans.

CHAMBER FORM AND COILING MODES

Although an extinct order and apparently confined to the Palaeozoic,* the order Fusulinida is one of the largest and most diverse groups of Foraminifera. The table of coiling modes (figure 4.3) brings out very well the dominance of planispiral coiling, 70 per cent of the total, and in particular, of fusiform chamber arrangement, found in almost half of the known genera and typical of the advanced fusulines. Many of these genera reach 1 cm length in the Permian and some reach a maximum length of 14 cm, among the largest Foraminifera known (Douglass, 1977). Compressed planispiral (or winding = plectogyral or streptospiral) arrangement tending to become uncoiled is characteristic of the smaller members of the order and reaches 21 per cent of the whole. Biserial-uniserial and uniserial make up 10 per cent. Trochoid arrangement, high and low together only some 5 per cent, is notably rare. Unilocular forms represent 6 per cent.

These differences in coiling modes are the basis of the distinction of the superfamilies and families in the microgranular group (see the Summary Classification at the end of the chapter). It is still too early to say whether differences in wall structure also distinguish the superfamilies, although many members of the Endothyracea are two layered and some may possess an inner tectorium. Some of the higher fusulines are basically three layered, while the two-layered genera are distinguished by an alveolar, inner layer or keriotheca (see below). Advanced forms are also distinguished by well-developed perforation.

Parathuramminacea

The unilocular genera are placed in the superfamily Parathuramminacea which includes the globular, or irregular, Parathuramminidae, the coiled, tubular Tournayellidae and the uncoiled Earlandiidae. The aperture is formed by the open end of the tube in the Tournayellidae and Earlandiidae and appears to be generally multiple in the Parathuramminidae. Advanced tubular forms show incipient and rudimentary septation and secondary deposits (chomata) have been noted in *Septabrunsiina* (Brenckle, 1973). Layered structure has not been discovered in this group to date.

Endothyracea

Small, multilocular fusulinids with streptospiral to planispiral coiling, together with uncoiled biserial and uniserial genera, are included in the superfamily Endothyracea. The family Endothyridae includes coiled forms and advanced genera with uniserial adult part. It is remarkable for the strong development of secondary deposits of calcite on the chamber floor (chomata) in genera such as *Endothyra* and *Quasiendothyra*. These may form mounds and spiny or hook-shaped projections (Brenckle, 1973; fig. 11). They may also be laid down where the septa abut the previous chamber and behind the septum above the aperture. The aperture is a low, median, basal opening becoming terminal and multiple in uncoiled forms. Infolding of the wall gives septal chamberlets which communicate with the exterior via septal pits in *Bradyina*. This genus is also perforate and cribrate.

Strongly built biserial to uniserial genera that closely resemble the members of the agglutinated Textulariidae are included in the Palaeotextulariidae. Cummings (1956) demonstrated conclusively that these are calcareous granular homeomorphs of the true textulariids, typically with two layers (figure 4.4), the inner with stacks of granules perpendicular to the surface. In some cases there is also a patchy, external agglutinated coating. The aperture is basal to terminal and cribrate in the uniserial adult part, as in *Climacammina*. In advanced forms the inner layer may be developed as internal buttresses and the multiple apertures may develop internal tubes or 'vestibular siphons'.

Compressed, biserial to uniserial genera with inverted or backward extending chambers are included in the Semitextulariidae. So far, the wall has been described as being composed of a single granular layer in this group. In *Semitextularia* the broad, inverted chambers become incompletely divided by vertical pillars.

Genera that are uniserial throughout are included in the Nodosinellidae, although differences in wall structure indicate a probable polyphyletic origin for this group. *Nodosinella* and *Frondilina* have two layers, whereas *Earlandinita* had been described as possessing a single layer.

Tetrataxacea

Multilocular fusulinids with trochospiral arrangements are included in the Tetrataxacea.

---

*Triassic records (Reitlinger, 1965; Zaninetti, 1976, 1977) may be the result of reworking or alternatively be of lituolids and require further study.

Although the species are abundant there are only a limited number of genera, included in the one family, Tetrataxidae. This is in great contrast to the agglutinating group. The wall structure in the Tetrataxidae is very similar to that of the Palaeotextulariidae and consists of two layers. Reduction of the chamber number in each whorl and the appearance of both horizontal and vertical partitions is seen in *Valvulinella*. Enrolled biserial forms which include the trochoid genus *Globivalvulina* are included in the family Biseriamminidae of Chernysheva (1941). The relation of this group to the other endothyraceans is unknown.

Fusulinacea

The typically large, planispiral-fusiform fusulinids with numerous chambers, or chambers subdivided by folds or septula, are included in the superfamily Fusulinacea. This was one of the most successful superfamilies of Foraminifera that ever existed and some 70 genera were recognised as belonging to it in the 'Treatise' (Thompson, 1964), a figure raised to over 100 by Ross (1967).

Although robust, the tests of this group generally show little detail externally and the last few chambers are often damaged. Orientated sections are therefore necessary for identification. Of these, the most useful are sections cut parallel to the axis of coiling, *axial sections* (as in figure 7.1C) and sections cut across the axis at the equator in the direction of coiling, *median* or *sagittal sections* (as in figure 7.1B). *Oblique sections* and *tangential sections* (parallel to the axis of coiling but not through the proloculus) may also be necessary to reveal other details.

As shown in figure 7.1A – C, the chambers are generally low (depressed) and reach from one end of the extended axis of coiling to the other (across the *equator* and from *pole* to *pole*). The traces of the septa on the external surface (where one chamber abuts another) are usually discernible as incised *septal furrows*. These give the characteristic rugby ball appearance to the fusuline test. The apertural face of the last chamber is referred to as the *antetheca*. It is represented internally by the septa of previous chambers. The external wall (and internal spiral septum) is known as the *spirotheca*. Both antetheca and spirotheca are finely perforate and true apertures are, apparently, not present.

The morphological features considered most important in classification are (1) detailed wall structure, (2) form of the septa, (3) character of chamber communications, and (4) character of the secondary deposits.

The wall appears to be of two basic types—the primitive, fusulinellid type and the advanced, schwagerinid or alveolar type. In the fusulinellid type there are three primary layers. These include an outer, rind-like film, the *tectum*, apparently dark with organic matter and an inner layer of clear calcite, the *diaphanotheca*. There is also an inner lining, tectorium or epitheca, of grey calcite (figure 7.1D). When the tectorium coats the floor of the chamber (the roof of previous whorls) the spirotheca here becomes secondarily, four layered. In the advanced, schwagerinid wall, the tectorium was lost and the diaphanotheca became coarsely alveolar, and is then termed the *keriotheca* (figure 7.1E). In vertical section this layer has a minutely bladed appearance and upper and lower keriotheca may be distinguished. Horizontal sections look like a honeycomb. Oxidised specimens of *Schwagerina campensis* from the Camp Creek Shales in Texas, in which a thin deposit of iron coats the wall and predates the internal matrix, reveal that the alveoli communicated with the pores of the tectum (Thompson, 1964).

The form of the septa is determined by the antetheca which may be plane, bow out in a curve or be corrugated or folded, as in figure 7.1A. In advanced members of the Fusulinidae and Schwagerinidae the septa became strongly folded or fluted, making an intricate pattern of loops when seen in axial section. This can often be seen in weathered specimens (figure 7.1B). The folding first appeared near the poles and at the base of the septa and migrated up the septa and to the equator in advanced forms. In the Schwagerinidae the septa became very strongly folded and eventually joined to form a regular network of lozenge-shaped chamberlets. The lobes and saddles (salients and re-entrants) may be resorbed where their tips meet, to produce tunnel-like *cuniculi*, running in the direction of coiling, as in *Parafusulina* (Thompson, 1948).

In the Neoschwagerinidae the chambers became subdivided by *septula* (sing. = septulum). These are downgrowths of the spirotheca and developed first in the spiral direction (transverse). More advanced genera also developed axial septula running the full width of the chambers as well as short secondary, spiral septula (figure 7.1G – I).

As has been noted, the antetheca appears to lack true apertures but the internal septa show single or multiple foramina that are formed by resorption of the wall. A single large foramen, or tunnel, is formed in the Fusulinidae and

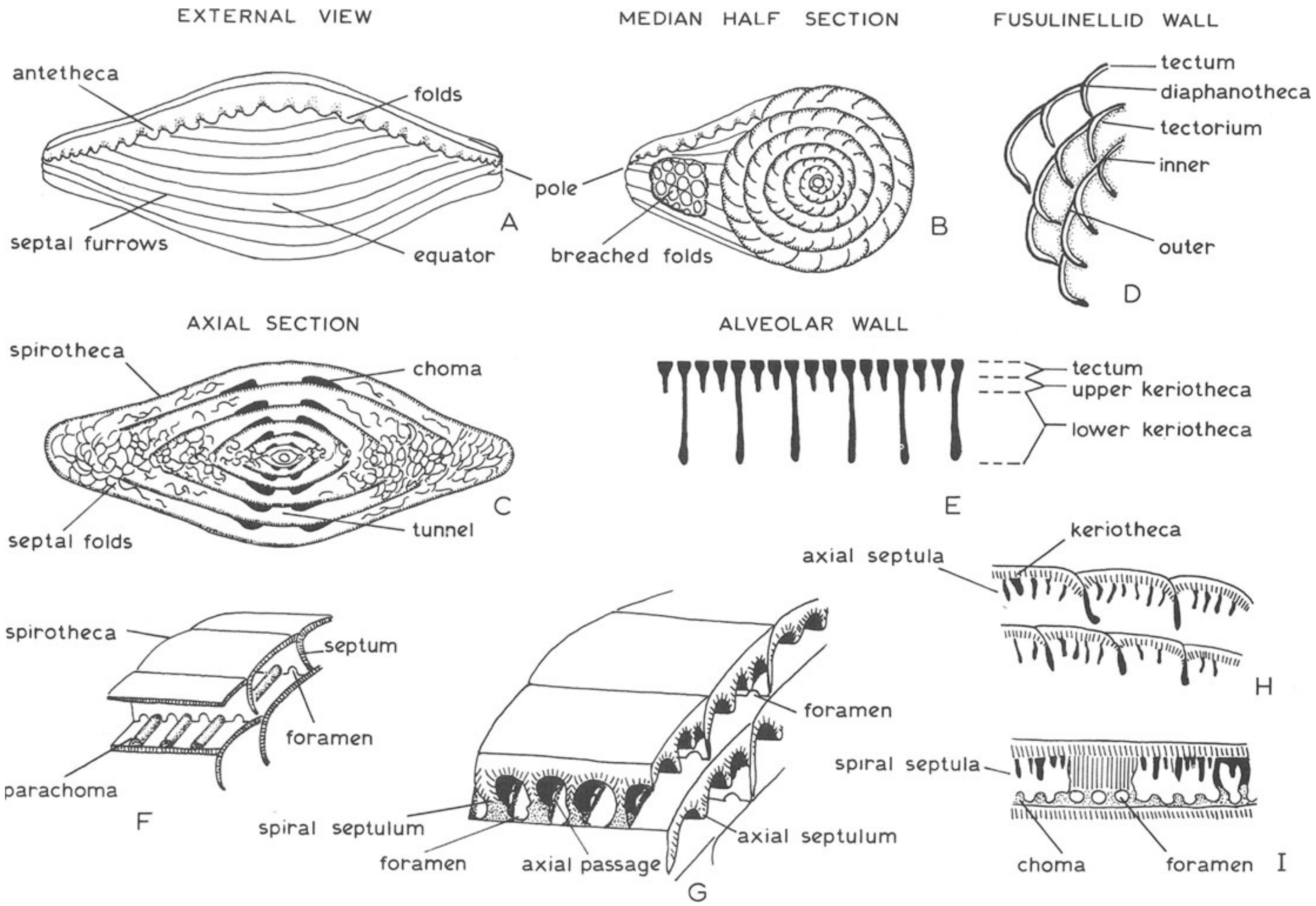

Figure 7.1 Fusulinacean morphology and terminology

A – C	External view, half-median section and axial section of a schwagerinid
D	Fusulinellid wall, showing tectorium in inner whorls only
E	Alveolar wall, much magnified to show pores of upper keriotheca penetrating tectum
F	Verbeekinid, showing continuous parachomata between foramina
G	Neoschwagerinid with primary spiral septula fused with the parachomata near septa and low axial passage. Two axial septula per chamber.
H	Advanced neoschwagerinid—portion of median section, showing numerous thin, irregular axial septula
I	Same—portion of axial section, showing primary spiral septula as roof pendants over axial passage and continuous with parachomata near septum, secondary spiral septula as roof pendants above multiple tunnels, foramina in portion of primary septum

Schwagerinidae, while multiple foramina are characteristic of the Verbeekinidae and Neoschwagerinidae.

The character of the secondary deposits is in part related to the form of the chamber communications. In the Fusulinidae and Schwagerinidae flanking, spiral *chomata* (ridges of secondary calcite) are laid down on the chamber floors so that in effect the tunnels connect a central grooved, channel system. In the groups with multiple foramina, smaller but multiple *parachomata* are developed (figure 7.1F). In the Neoschwagerinidae these spiral parachomata link with the primary spiral septula in the roof to form partitions that are complete, except for a central axial passage that maintains communication along the chamber (figure 7.1G). The chamber is then divided into a series of elongate chamberlets, each of which is again partially subdivided into box-like cellules in the roof. Secondary deposits of calcite are also laid down along the axis of the test, particularly towards the poles.

Figure 7.2 shows how these morphological characters in combination are diagnostic for the different families of fusulines. It is not possible to distinguish the families by wall structure alone, and as has been noted there are particular difficulties in the Ozawainellidae which are generally found recrystallised. Although some members of the *Staffella* group appear to have a schwagerinid wall there appears to be no way of consistently separating this group from the ozawainellids which include *Millerella* and '*Eostaffella* (=*Paramillerella*). Therefore, following Dunbar (1963) these genera are grouped together. The *Schubertella* group is distinguished by a switch in the angle of coiling in the adult whorls. As the other features of the test resemble those of the Fusulinidae they are best regarded as a subfamily, following Thompson (1964).

Archaediscina

Apparently standing apart from the microgranular fusulinids are a group of families in which the outer layer is radial hyaline in structure. In a number of species referred to *Archaediscus* (or related genera, Brenckle, 1973) the inner granular layer appears to be absent. This suggests that its presence may be due to secondary alteration, in those cases where it occurs, and that this group may be closer to some of the early hyaline families than to the other fusulinids.

Unilocular genera are placed in the Archaediscacea which includes both streptospiral to planispiral forms and conical forms with umbilical fillings and septal bridges. Multilocular uniserial genera are placed in the Colaniellacea. Advanced forms in this group develop vertical partitions. An interesting feature shown by some species of *Archaediscus,* such as those placed in the separate genus, *Asteroarchaediscus,* by some workers (see Brenckle, 1973), is the corrugation of the tube to give a stellate cross-section and close the aperture. There may be a link here with the radiate aperture of *Colaniella.*

POSSIBLE EVOLUTIONARY RELATIONSHIPS

The most primitive superfamily is the *Parathuramminacea* and it seems logical to suppose that these simple forms give rise to the higher fusulinids via genera with incipient septation. However, as we have seen, in part due to the problem of recrystallisation, a number of doubtful genera have been included in this group in the past and if these are excluded it appears that good records are confined to the Upper Palaeozoic. In addition, the stratigraphical record, outside Russia, is still insufficiently detailed to provide definite support for the lines of descent suggested by morphology alone.

According to Lipina (1959) the tournayellids show progressive evolution of septation, leading to *Septatournayella* and finally to the endothyrid stage. Similarly, Reitlinger (1958) considers that the endothyrids developed from the tournayellids in the Devonian and thereafter descended in parallel. A likely ancestor for the tournayellids is *Pseudoglomospira* which provides a direct link with the Ammodiscidae. A possible line of descent is via *Brunsiina* with streptospiral initial part and, later, planispiral whorls with poor septation, like *Tournayella.* But although *Brunsiina* is present in the Upper Devonian the most ancient tournayellids, according to Dain and Grozdilova (1953) are *Tournayella* and *Septatournayella* which appear in the Middle Devonian. This could be taken as evidence for direct descent from *Ammodiscus* and the possibility of polyphyletic descent from both streptospiral and planispiral, granular ancestors.

The tournayellids have not been discovered so far in the Devonian of North America and do not appear until the Tournaisian, the time of their acme in Russia. *Brunsiina, Septabrunsiina* and *Septatournayella* appear in the lowest Tournaisian

FAMILIES OF FUSULINACEA	WALL STRUCTURE	CHARACTER OF SEPTA	CHAMBER COMMUNICATIONS	SECONDARY DEPOSITS	SEPTULA
OZAWAINELLIDAE (inc. STAFFELLIDAE of authors)	poorly known ?advanced genera 'fusulinellid' or even 'schwagerinid'	plane	tunnel	chomata	None
FUSULINIDAE (inc. SCHUBERTELLIDAE of authors)	'fusulinellid'	weak to moderate folding	tunnel	chomata and axial deposits	None
SCHWAGERINIDAE	advanced type 'schwagerinid'	moderate to strong folding	tunnel	chomata and axial deposits	None
VERBEEKINIDAE	'schwagerinid'	plane	multiple foramina	parachomata	None
NEOSCHWAGERINIDAE	'schwagerinid'	plane	multiple foramina	parachomata	spiral and axial

Figure 7.2 Diagnostic features of the fusulinaceans

Foram Zone 7, uppermost Kinderhook and lowest Osage, prior to *Tournayella* in the uppermost Osage, Zone 8 (Skipp *et al.,* 1966; Sando *et al.,* 1969; Brenckle, 1973). *Tournayella* also ranges higher than most of the other genera, persisting to the base of the Chester (Foram Zone 15, Upper Visean). This led Skipp *et al.* (1966) to suggest that the non-septate *Tournayella* is really the most advanced member of the family. Pursuing this idea, they speculate that the tournayellids may be a branch of the Endothyridae and are really septate, but that resorption, along with diagenetic recrystallisation, has masked the septation. Apart from the fact that this argument would appear to destroy the basis on which the different genera are recognised, it makes it necessary for them to explain away the Devonian representatives in the USSR as an evolutionary side-line, rather than admit them as ancestral. The student should take note here of the difficulties that arise in attempting to work out evolutionary relationships from local range zones. These may reflect the true life ranges (biozones) only partially and, indeed, be quite misleading.

As the earliest record for the endothyrids is that of *Quasiendothyra,* also in the Middle Devonian of Central Asia (Rauzer-Chernousova and Reitlinger, 1957; Fursenko, 1959a), Glaessner (1963b) considers both the Tournayellidae and the Endothyridae are independent offspring of the Ammodiscidae. Reitlinger (1958, 1966) however, as noted, prefers the idea that the endothyrids sprang from the tournayellids and then developed along parallel lines. The Devonian endothyrids in the USSR appear to have been more or less planispiral species. The number of species much increases in the Tournaisian and they are dominantly plectogyral with a range of types of secondary deposits, including hooks, ridges and beads. They reach their acme and largest sizes in the Visean with trends towards evolute, planispiral growth, *Loeblichia* and cribrate apertures, *Cribrospira.*

Skipp (1969) records a similar Tournaisian fauna of plectogyral species in the Redwall Limestone, Arizona with 'spectacular' secondary deposits in species such as *Endothyra spinosa* and *E. bellicosta.* Large forms with moderate skew coiling also appear, such as *E. trachida* which she believes may be ancestral to *Eoendothyranopsis* in the upper part of the Redwall Limestone (Visean).

The first palaeotextulariids also occur in the Lower Carboniferous, and *Palaeospiroplectammina* which appears to be the ancestral form was described by Lipina (1965) from the Tournaisian of the USSR. Species belonging to this genus have also been discovered in the Tournaisian of Belgium (Conil and Lys, 1964) and Arizona (Skipp, 1969). The initial coil and two-layered wall indicate a possible origin from a planispiral endothyrid. The genus gave rise to *Palaeotextularia* in the Tournaisian which in turn gave rise to *Palaeobigenerina* and related genera in the Visean, with completely uniserial descendents in the Permian (Cummings, 1956).

The two-layered wall of the tetrataxids also suggests affinity with the endothyrids but so far no links have been discovered between these two groups. The Tetrataxidae, like the Endothyridae and the Palaeotextulariidae reach their maximum abundance in the Visean. Advanced genera such as *Bradyina* and *Globivalvulina* also appear in rocks of this age.

The Archaediscidae also reach their maximum abundance in the Visean but their possible phylogenetic relations with other families of similar wall structure is problematical, because complex uniserial genera appear both early, in the Devonian, and late, in the Permian.

Although there are differences in detail, due to differences in approach to the taxonomic problems involved, there is now a general consensus concerning the rise and main lines of development of the Fusulinacea. Thus most authors now seem to agree with Glaessner (1945, see reprint 1963a) that the fusulines descended from the endothyrids via an intermediate group that includes *Staffella* and its allies, Ozawainellidae as here understood (Rauzer-Chernousova and Reitlinger, 1957; Dunbar, 1963; Rauzer-Chernousova, 1963; Ross, 1967). Supporting evidence is provided (1) by the apparent similarity in wall structure between late endothyrids and the ozawainellids in that some already have 'fusulinellid' or even 'schwagerinid' walls; (2) by strong development of secondary deposits in both groups; (3) by the rise of the Ozawainellidae in the later, Lower Carboniferous (Visean) prior to the development of the fusulines in the Upper Carboniferous; (4) by the increase in size and number of whorls shown by the subgenera of *Staffella,* with the spherical species showing elongation of the axis of coiling and an approach to the typical fusuline form (Rauzer-Chernousova, 1963, fig. 1).

As shown by figure 7.3, the Fusulinidae arose from *Staffella (Eostaffella)* at the Lower Carboniferous – Upper Carboniferous boundary. This family showed a rapid proliferation of genera, with increasingly strongly folded septa, which dominated the lower part of the Upper Carboniferous. Numbers decline thereafter but the family persisted into the Upper Permian.

The Schwagerinidae arose from *Fusulina* in the uppermost, Upper Carboniferous (Moscovian – Gzelian boundary) and evolved slowly until the end of the period with the moderately folded *Triticites* dominant. In the Lower Permian a dramatic burst of evolution produced some 20 new genera of schwagerinids, characterised by intense folding of the septa which fuse to form chamberlets and cuniculi. Inflation of the chambers, sometimes only in the adult whorls, as in *Pseudoschwagerina,* is also characteristic. Most of these genera become extinct in the early, Middle Permian but some persist and peculiar forms with reduced, single-layer wall, such as *Polydiexodina,* do not appear until the Middle Permian.

The Verbeekinidae also evolved from *Staffella* but via the intermediate form *Sphaerulina,* near the Lower Permian – Middle Permian boundary (Kanmera, 1957; Rauzer-Chernousova, 1963; Leven, 1964; Ross, 1967) or *Pamirina* (Kanmera *et al.,* 1976). There was rapid evolution of this group in the lowermost Middle Permian (Artinskian) to *Eoverbeekina* and through *Misellina* to *Verbeekina* which have a complete system of foramina in each chamber. The parachomata are saddle shaped in *Misellina,* discontinuous in *Verbeekina* (Morikawa, 1965).

The Neoschwagerinidae may have arisen directly from *Cancellina,* in which spiral septula first appear, but the *Sumatrina* group are considered to have sprung separately from *Misellina*. This rapid evolution was followed by almost equally rapid extinction and both families disappeared abruptly at the end of the Middle Permian.

To summarise the main evolutionary trends exhibited by the Fusulinacea, these include: a general increase in size, combined with chamberlet formation by septal folding or insertion of septula; development of the 'honeycombed', alveolar wall with loss of the epitheca; replacement of the central tunnel by numerous foramina. Very large size in the Lower Permian is connected with extremes of dimorphism, the very large individuals known, some up to 6 cm length, being microspheric. Axial infilling is also common in the larger species.

ECOLOGY

The ecological relationships of extinct groups of Foraminifera have to be inferred by analogy with morphologically similar groups of Recent Foraminifera and by study of the associated organisms and enclosing sediment. In the discussion on the ecology of agglutinated forms we have seen the difficulties of interpretation that can arise even in cases where the genera are still living. Interpretation becomes doubly difficult where the entire order and most of the associated organisms are extinct. Nevertheless, much has been learned about the distribution and the sedimentary and biofacies relationships of the fusulinids. This becomes quite revealing when combined with an assessment of their morphology.

The wide variety of coiling modes in the order (figure 4.3) indicates a large number of different life strategies and probable adaptation to a broad range of sedimentary environments. However, the very high percentage of planispiral (inc. plectogyral) coiling, almost three-quarters of the whole, indicates that certain adaptations were particularly successful.

The dominant planispiral group are the large fusulinaceans, more than half of the whole if all the genera suggested are accepted. As shown in chapter 4, Larger Foraminifera appear to be confined to shallow waters in the tropics and subtropics today, down to some 80 m depth, and show many features that can be interpreted as adaptations to a symbiotic mode of life.

The fusulinaceans occur only in the open marine phases of the Pennsylvanian cyclothems of North America (Thompson, 1964) and they appear to have been essentially shallow water (Ross, 1969, 1971, 1972a, 1978a; Lagenheim *et al.,* 1977). Thus in his study of the palaeo-ecology of *Triticites* in the Upper Pensylvanian of Texas, Ross found that relatively large, fusiform species occurred in shallow water, algal meadows and associated with banks of crinoid fragments. Elongate species occurred in shallow bays and lagoons, whereas small, fusiform species occurred in slightly deeper water to wave base. Very few occurred in sediments interpreted as deep water.

The very wide geographical occurrence of the fusulinaceans from Ellesmere Island, Canada to Patagonia and North Island, New Zealand (Thompson, 1964) may appear to contradict the idea that they were tropical forms, but this broad range is probably an indication of a much wider tropical – subtropical belt in the Upper Palaeozoic and relatively warm conditions world wide. Ross has shown, by analysis of the growth pattern, that *Schwagerina silverensis* and *Pseudoschwagerina robusta* had two unequal periods of growth per year, indicating that Arizona and West Texas were in the solar tropics in the Lower Permian. *Eoparafusulina yukonensis* from N.W. Canada had only

		U.S.A.	U.S.S.R.	CHINA	JAPAN	FUSULINID ZONES
PERMIAN	UPPER	Ochoan	Dorasham	Changhsing	Mitaian	Palaeofusulina
			Dzhulf.	Wuchiaping	Kuman	Codonofusiella
			Abadeh.			
	MIDDLE			Maokoun		Lepidolina
		Guadaloupian	Kazanian		Akasakan	Yabeina
						Neoschwagerina
		Leonardian	Artinskian		Nabeyaman	Cancellina
				Chihsia		Misellina
	LOWER	Wolfcampian	Sakmar.	Mapingian	Sakamotozawan	Pseudofusulina
			Asselian			Pseudoschwagerina
CARBONIFEROUS	UPPER	Missour. Virgil.	Gzhelian			Schwagerina
					Hikawan	Triticites
		Des Moins.	Moscovian		Kurik.	Fusulina
		Atokan			Akiyoshian	Fusulinella
			Namur. Bashkir.		Atetsuan	Profusulinella
		Morrowan			Kamitakaran	Pseudo staffella
						Millerella (Eostaffella)

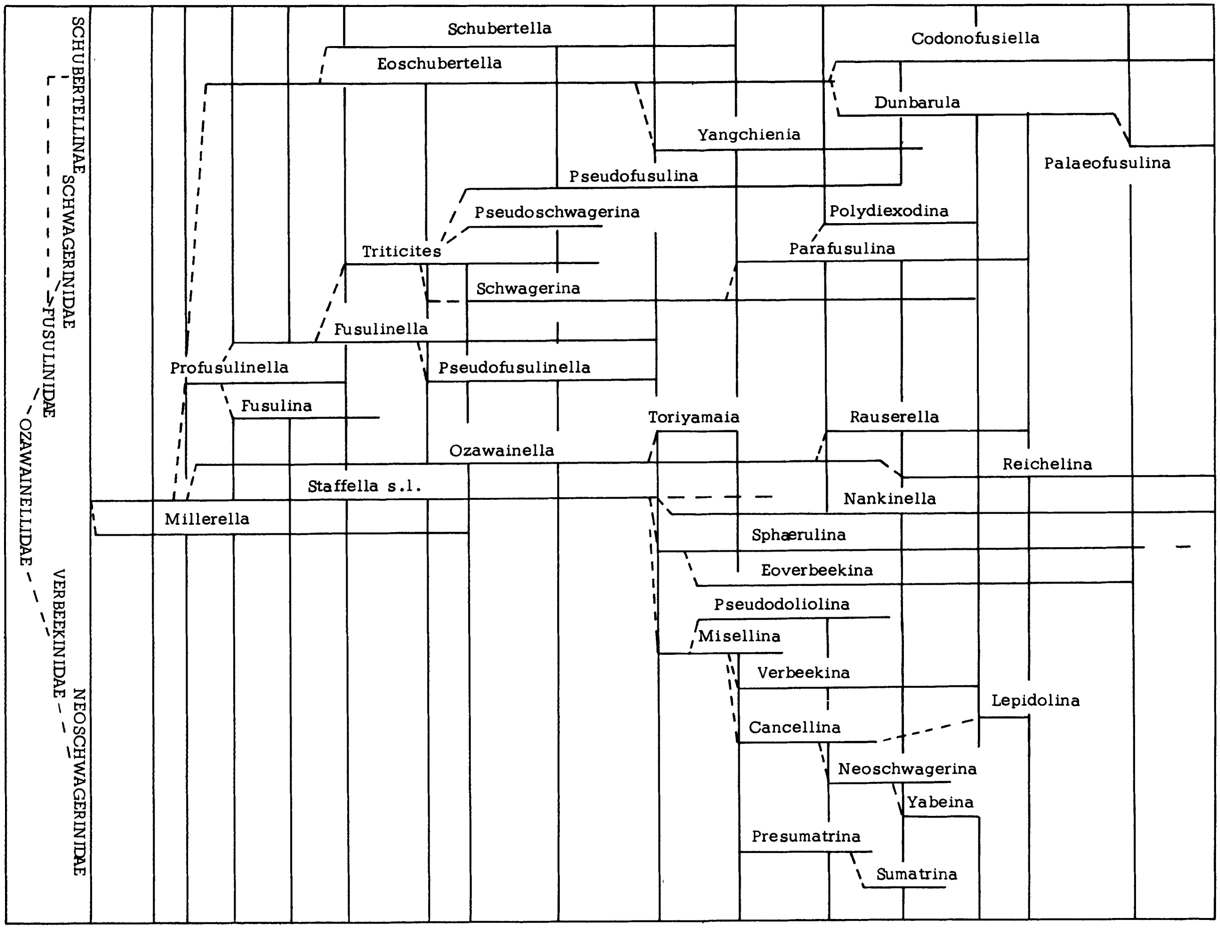

Figure 7.3 Phylogeny of the fusulinaceans. Data largely drawn from Kanmera *et al.* (1976). Note that a Schwagerina Zone is now recognised at the top of the former Triticites Zone and below the Pseudoschwagerina Zone, that is at the very top of the Carboniferous. Previously, the ranges of *Schwagerina* and *Pseudoschwagerina* have been considered to be the same (see also Douglass, 1977).

one nearly uniform period of growth per year, indicating a position outside the solar tropics.

The fusulines exhibit the typical fusiform, roller shapes also shown by the alveolines, a known symbiotic group. They also show striking morphological trends that can be interpreted (see chapter 4) as adaptations to this mode of life. As pointed out by Ross (1974): 'the resulting structure does provide chamberlets, or small spaces, near exterior pores of sufficient size to permit a symbiont to occupy a thin walled portion of the shell without loss of shell strength, and these structural trends are accompanied by a general increase in size of the species.' The apparent lack of true apertures, as in *Nummulites,* may indicate that symbiosis was obligatory—see chapter 2.

Compressed, planispiral (plectogyral) coiling is the dominant mode in the smaller fusulinids and characteristic of the Endothyridae, the most abundant family. Both the tournayellids and endothyrids are abundant in nearshore and shelf limestones (Ross, 1973). Although Cummings (1961) suggested a 'semi-pelagic' habit for them, Betty Skipp (1969) on the basis of her studies of the Redwall Limestone, Arizona considered them benthonic forms flourishing in a warm, shallow, moderately high energy environment. Most occurrences were in coarse-grained, skeletal, oolitic and peloidal limestones (of rounded bioclasts). Some species occur in particular facies. Thus *Endothyra trachida* is most common in coarse-grained, bioclastic limestone with appreciable transported crinoidal debris. Species with well-developed secondary deposits, such as *E. spinosa* and *E. bellicosta* (mentioned above) occur in oolitic and bioclastic limestones with little crinoidal debris. She relates the distribution of these forms to the presence of 'crinoid gardens'. Because these species are generally well preserved, she considers they have not been transported far and actually lived on these limestone substrates. However, good preservation is no guide to lack of transport on the shallow shelf today and it seems likely that these faunas, particularly those in the oolites, are transported death assemblages. Analogy can be made with modern planispiral genera such as the *Elphidium* group which occur on the shallow shelf as deposit feeders on the sea bed in relatively quiet areas and as epibionts in high energy zones. We may suppose that the endothyrids of the Redwall Limestone lived as vagrants clinging by their pesudopods to various plant and animal substrates, crinoids, byrozoans, etc., and on death accumulated in the bioclastic limestones and oolites. The secondary deposits may represent an attempt to stabilise the test under turbulent conditions. As the fusulines evolved from this group it is possible that the endothyrids were also symbiotic. In this connection, the similarity between the septal folds and septal pits in *Bradyina* and *Elphidium* is thought-provoking. This mode of life would explain their 'almost exclusive' occurrence in the euphotic zone, reported by Mamet (1977). It is significant that all the Foraminifera in Carboniferous turbidites are size sorted and occur in the graded beds. None have been found in the autochthonous, pelagic facies.

The uncoiled planispiral forms, the biserial to uniserial and the uniserial genera (10 per cent of the whole) probably represent adaptations to an infaunal life, as known in the agglutinating group. A number of these genera possess patchy agglutinated coats.

Trochoid coiling, both high and low, is rare in the fusulinids, showing a lack of development of fixed and temporarily attached genera apart from the tetrataxids. Although limited in number of genera this group is abundant world wide. They occur particularly in marine limestones, particularly sandy limestones (Cummings, 1961) and have been found in a variety of associations including calcareous algae and cornuspirinids, possibly originally attached to seaweed (Henbest, 1963). They also occur attached to corals, such as *?Corwenia* from the Lower Carboniferous, D_2, at Hafod-y-calch, N. Wales. Cossey (pers. comm.) has also found *Tetrataxis* attached to corallites within a single colony of *Lithostrotion junceum,* from the L. Carboniferous, B_2, of Cave Dale, near Castleton, Derbyshire, as well as to *Caninia.* A similar association is reported by Toomey and Cys (1979).

STRATIGRAPHICAL USE OF THE FUSULINIDS

The abundance and continuous evolutionary development of the order through the Upper Palaeozoic, over a 120 million year period, makes it one of the most useful groups of Foraminifera for stratigraphical correlation. Emphasis has traditionally been placed on the large fusulinaceans, but pioneer work on the smaller fusulinids began in 1930 in the USSR and soon proved their importance. By the 1950s a number of broad zones were recognised in European Russia, across the Russian Platform to the Urals, 5 in the Tournaisian and 9 in the Visean (Rauzer-Chernousova and Reitlinger, 1957; Reitlinger, 1958). Interest grew more slowly in the West but gathered pace after the work of Zeller (1950, 1957) in the USA and Cummings (1955, 1956) in Great Britain. Research into the group then became international: Belgium (Conil, 1963; Conil and Lys, 1964, 1965, 1966, 1967, 1968; Mamet, 1965; Mamet *et al.*, 1965; Legrand *et al.*, 1965), France (Mamet, 1968a), Scotland (Cummings, 1961) Wales (Brown, 1960; Nichols, 1961), Canada (McKay and Green, 1963), USA (Skipp, 1961, 1969; Skipp *et al.*, 1966), Morocco (Mamet *et al.*, 1966), Egypt (Omara and Conil, 1965). This work showed that many genera were cosmopolitan and that the ranges of a number of species are virtually the same in the North American Cordillera as they are in the USSR. Further work has shown that the 15 foraminiferal zones recognisable in the Lower Carboniferous and Namurian of Belgium can be correlated into the American Cordillera and form the basis of a worldwide scheme (Armstrong *et al.*, 1970; Brenckle, 1973; Mamet, 1968b; Mamet and Skipp, 1970; Petryk *et al.*, 1970; Sando *et al.*, 1969). Figure 7.4 shows how accurate correlation can now be made between the European and American stages.

Mamet (1977) considers that the global zones should be based as far as possible on the joint first appearance of members of different phylogenetic groups, i.e. the passage between zones 9 and 10 which marks the Tournaisian/Visean boundary. The Tournayellidae *(Septabrunsiina, Tournayella,* etc.) largely disappear at the boundary, while the first members of the Palaeotextulariidae, Tetrataxidae and Biseriammidae appear in the latest Tournaisian, together with forms he regards as *Endothyra* s.s.

In contrast to the smaller fusulinids, the large fusulinaceans are a group long favoured in stratigraphy. Rapid evolution along a number of different lines, with marked morphological trends, combined with wide geographical range, makes them 'one of the most reliable groups for long range as well as local correlations within the Pennsylvanian and Permian Systems' (Skinner and Wilde, 1965). They also tend to occur in vast numbers, which gives them an advantage over other reliable index fossils such as the ammonoids. These advantages, coupled with large size, have made them an active object of research since the pioneer investigations of Fischer (1829, 1837) who gave the name *Fusulina* to the 'fossil wheat' of the Moscow Carboniferous—see Kahler and Kahler (1966) and Douglass (1977). By the turn of the century fusulinaceans had been discovered world wide. Classic studies include: the first well-illustrated taxonomic study on material from China and Japan (Schwager, 1883a); Permian fusulines from the Carnic Alps (Schellwien, 1898); the first major global stratigraphical synthesis (Deprat, 1912) and the updated version by Colani (1924). The first major study in N. America was on the Permian by Dunbar and Condra (1927), with later work on the Permian of Texas (Dunbar and Skinner, 1937) and the Upper Carboniferous of Illinois (Dunbar and Henbest, 1942).

In the decades since World War II, research on the superfamily has intensified. In N. America further work has been done on the U. Carboniferous of Texas and New Mexico (King, 1973) and also on the Permian of Texas (Ross, 1963), California (Skinner and Wilde, 1965), British Columbia (Ross and Bamber, 1978; Ross and Monger 1978), the Yukon (Ross, 1978b), Alaska (Petocz, 1970) and Ellesmere Island (Nassichuk and Wilde, 1977). In Europe and Asia, studies on Carboniferous fusulines include the Urals (Rauzer-Chernousova, 1961) and Spain (Ginkel, 1965, 1973) and studies on the Permian include Japan (Toriyama, 1967; Kashima, 1973), Thailand (Toriyama *et al.*, 1974; Toriyama, 1975), Pakistan (Douglass, 1970), Iran (Bozorgania, 1973) and Iraq (Lloyd, 1963).

The simplified evolutionary tree (figure 7.3) shows that there are a number of genera of short geological time range or distinct time of acme, which allow a broad, worldwide scheme of some 16 zones to be distinguished. As is to be expected, these zones are not equally well developed everywhere and there also appears to be a tendency towards the development of faunal provinces (see below). For instance, although there is a distinctive sequence from *Profusulinella, Fusulinella* to *Fusulina* in the USA, the first appearances of *Fusulinella* and *Fusulina* appear to be almost synchronous in the USSR. In practice, correlation depends not simply on the use of generic range zones but on first occurrences and acme zones in combination with faunizones (based on distinctive assemblages) and concurrent range zones (based on overlapping ranges of particular index fossils). Zones based on the ranges of species of verbeekinids have been established in China (Sheng, 1963) and Japan (Toriyama, 1967) but according to Gobbett (1967) these cannot be applied to the whole Tethyan area. He considers it necessary to establish broader divisions to allow correlation on a regional scale and has attempted to do this on the basis of the three main phases of verbeekinid evolution represented by the successive, *Misellina, Neoschwagerina* and *Yabeina* faunas. Further detailed work, especially by workers in the Far East (Kanmera *et al.*, 1976), allows the broad zonation shown in the figure for the Permian. The difficulties still hampering application of a world-

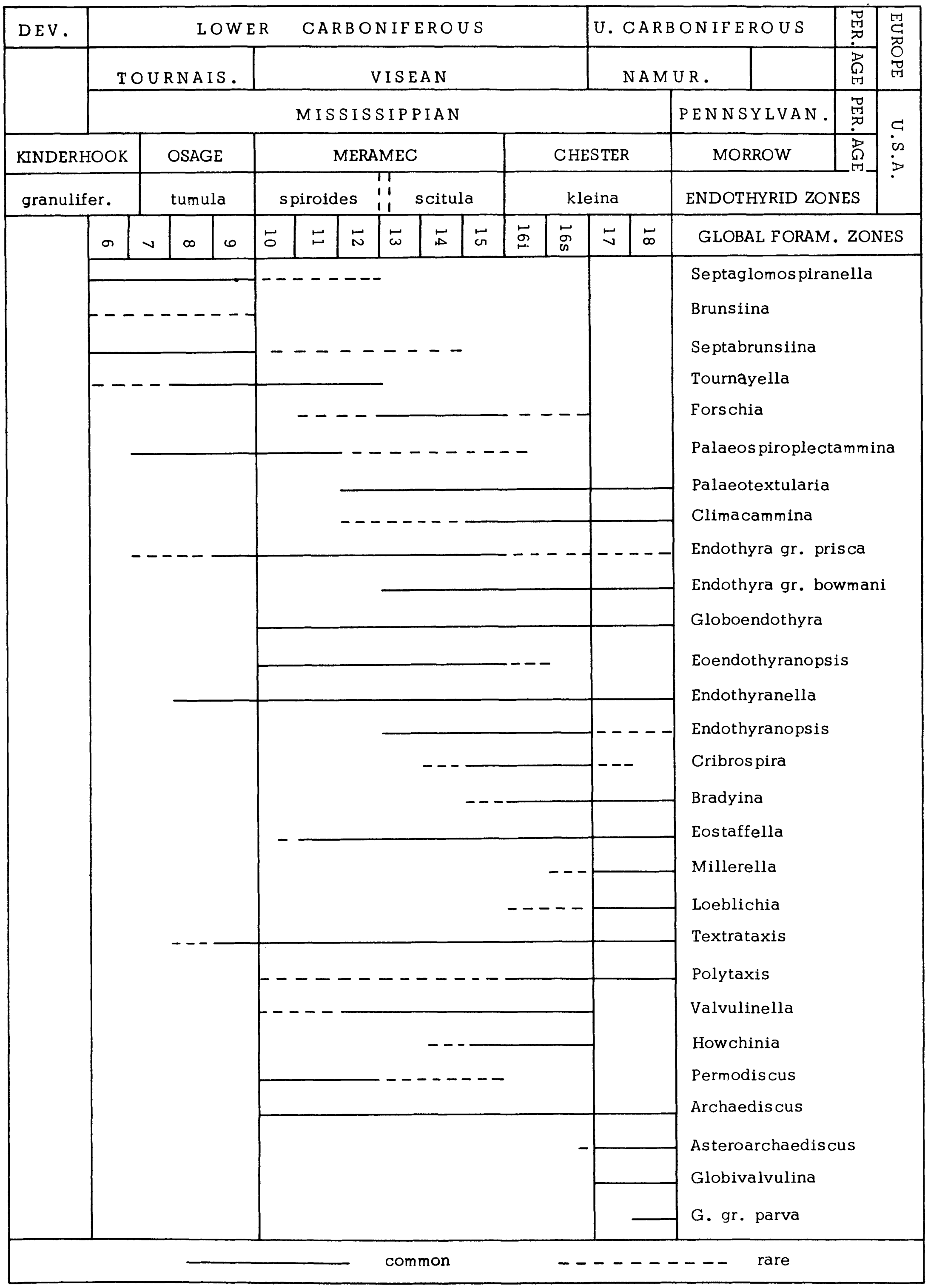

Figure 7.4 Worldwide stratigraphical ranges of important, smaller fusulinid genera and species groups, showing correlation between the American and Eurasian standard Lower Carboniferous successions based on the 'global foram zones'. Data drawn from Mamet and Skipp (1970) and Brenckle (1973)

wide scheme are admitted by Douglass (1977), who states that the generic zones tend to be defined in terms of the stratigraphical series or stages and are therefore subject to the problems encountered in the definition of such boundaries. This also leads to circular reasoning involving stages based on zones and zones based on stages, which must be avoided.

FAUNAL REALMS IN THE UPPER PALAEOZOIC

The success of the fusulinids in worldwide correlation depends upon the existence of many cosmopolitan genera, but there are also a number of other genera and species that appear to be geographically restricted. Persistence of these provincial differences through long intervals of time has been taken by Ross (1967, 1973) to indicate the existence of definite faunal realms.

Two major realms can be distinguished: a Tethyan – Boreal realm including Eurasia and extending across the Arctic into the northern Cordillera, and an American Mid-continental and Andean realm. The differences between these two major realms were more marked at certain times when isolation prevented free interchange. Also, at certain periods the Eurasian realm became markedly differentiated into Tethyan and Boreo-arctic subprovinces (Lippina and Reitlinger, 1970), probably indicating the former tropical and extratropical regions. This has led Mamet (1977) to distinguish three realms: (1) Tethyan, including the British Isles; (2) Taimyr – Alaskan; (3) Kusnets – N. American, including Japan. Ross (1973) has related these realms to the pre-drift positions of the continents.

During most of the Lower Carboniferous the fusulinid microfaunas were nearly cosmopolitan but the American Midcontinental province showed much less diversity and more associated agglutinated species. Tethys appears to have been the main breeding ground with about 800 species identified, many with complete evolutionary sequences. Endothyrids are particularly common in algal limestones, making up some 3 – 5 per cent of Koninckopora 'grainstones' and occasionally reach 20 per cent. Least provinciality appears to be shown by the faunas of the early Visean, but in the middle and late Visean the two major realms are recognisable. The Eurasian province is characterised by abundant *Eostaffella, Bradyina,* palaeotextulariids, *Valvulinella* and *Howchinia;* the Midcontinental province by abundant *Eoendothyranopsis,* rarity of palaeotextulariids and absence of *Valvulinella* and *Howchinia.* *Eostaffella* is not abundant until the late Visean. In the Namurian these differences become more marked and correlation difficult. *Bradyina* does not occur in N. America until the latest Namurian.

In the Upper Carboniferous the development of the fusulinaceans differs in the two provinces. There are more genera in the Eurasian province and some common genera show different ranges. In the Gzelian the schwagerinids evolve rapidly in the Eurasian province but only some of them invaded the Midcontinental province; an example is *Triticites* which apparently produced local lineages.

In the Lower Permian a largely cosmopolitan fauna developed with 11 genera common to the two major realms (Gobbett, 1973), but the Boreal subprovince retains individuality because of the persistence there of certain long-ranging Fusulinidae. The appearance of new genera such as *Acervoschwagerina* and *Toriyamaia* in Japan also give a distinctive character to the eastern part of the Tethyan subprovince. During this time, as in the Lower Carboniferous, there was full connection between the Urals seaway and Tethys and across the Arctic to the Cordilleran seaway as a result of general submergence.

In the lower part of the Middle Permian (Artinskian – Kungurian) regression led to the re-establishment of the Eurasian and American Midcontinental realms. The Tethyan subprovince developed separately from the Boreal province which was impoverished with only cosmopolitan genera. A large number of new taxa now appeared apparently endemic to the Old World Tethys, including *Pisolina, Yangchienia* and the verbeekinids. There was now also migration of some genera, including *Eoverbeekina* and *Misellina,* into Central America, apparently from the western end of Old World Tethys.

The fusulinaceans disappeared from the Boreal subprovince by the late Middle Permian and are restricted to Tethys and the American Mid-continental Andean realm with an extension into the northern Cordillera. Faunas were more diverse at this time in Tethys than at any time in the Permian, with complex schwagerinids and verbeekinids; 22 genera were apparently endemic. *Yabeina* and *Neoschwagerina* also reach North Island, New Zealand, as well as the northern Cordillera (figure 7.5).

The schwagerinids and verbeekinids became extinct at the end of the Middle Permian and fusulines are restricted to central and eastern Tethys in the Upper Permian. No new genera appear and the fauna consists of small ozawainellids and schubertellids only.

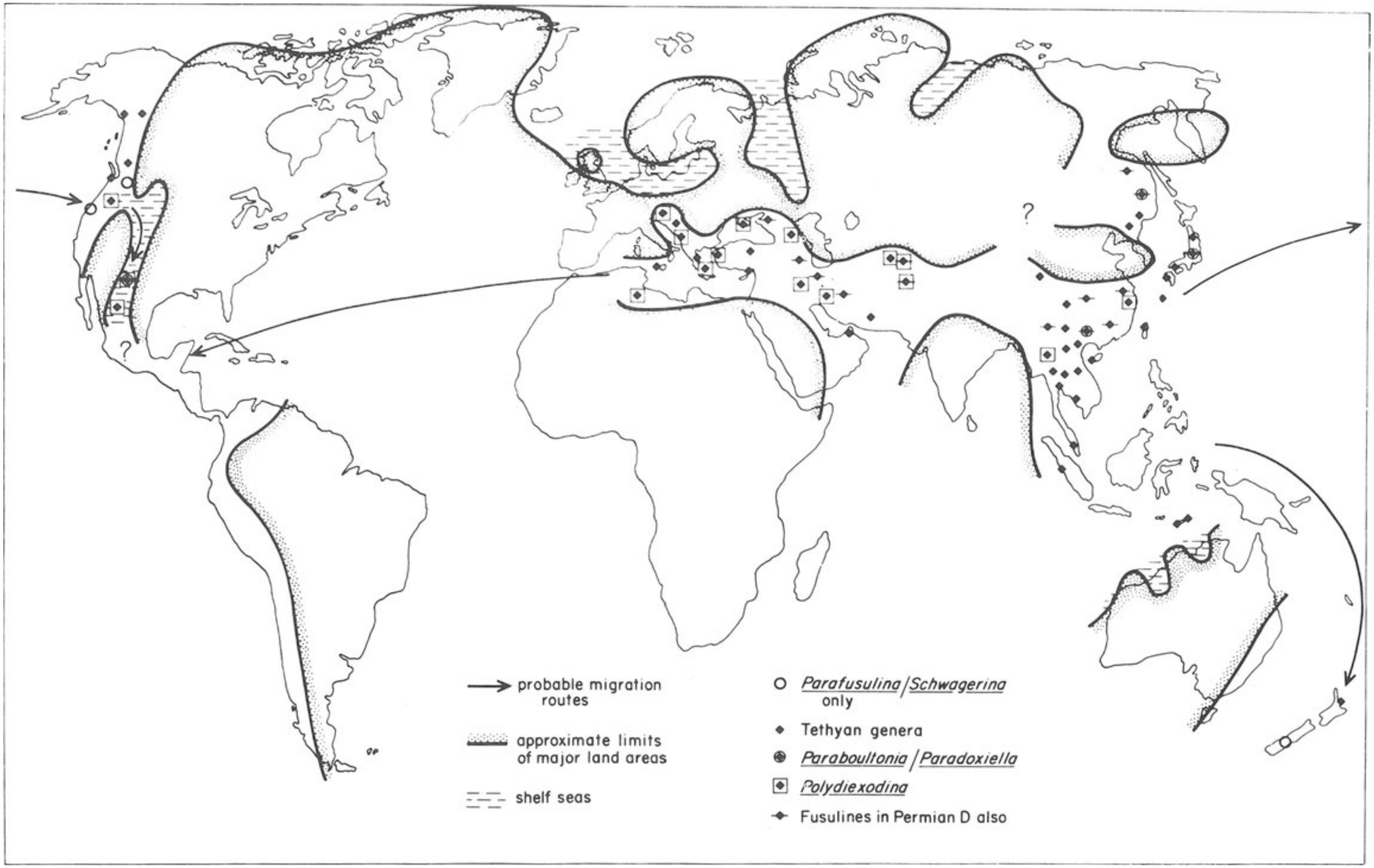
probable migration routes
approximate limits of major land areas
shelf seas
○ *Parafusulina*/*Schwagerina* only
◆ Tethyan genera
⊛ *Paraboultonia*/*Paradoxiella*
▣ *Polydiexodina*
-◆- Fusulines in Permian D also
?

Figure 7.5 Distribution of fusulinaceans in the late Middle Permian, with disappearance from the Boreal subprovince and migration of Tethyan genera to New Zealand and the Cordillera. From Gobbett (1973)

The student is bound to be impressed by the rich diversity of Upper Palaeozoic fusulinid assemblages, by the remarkable display of evolutionary trends and the possibilities of stratigraphical application in correlation and palaeogeography. However a warning note is necessary; enthusiasm must be laced with caution. As emphasised at the beginning of the chapter, problems caused by recrystallisation often make classification uncertain, even at family level, as in the case of the 'staffellids'. Groupings have then often been made on grounds of supposed evolutionary relationships rather than strictly on morphology. Great care should be taken in interpretation of random thin sections (following Cummings, 1958) and new taxa should not be founded on such material. Attention should be given to the complaint of Gobbett (1973) that many fusuline species have been diagnosed on small samples without much attempt to work out the growth stages and compare them with similar species. Some species and even some genera have been distinguished on size alone. With the general failure to apply the modern species concept this means that polytypic species have been split into species, each then, apparently, with restricted geographical distribution. Gobbett goes so far as to say that the uncertain validity of many species makes it impractical to discuss fusuline distribution at the specific level. Nevertheless as stated earlier, proper discrimination of species is essential to stratigraphical work, not least in solving problems of endemism and provincialism.

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SUMMARY CLASSIFICATION

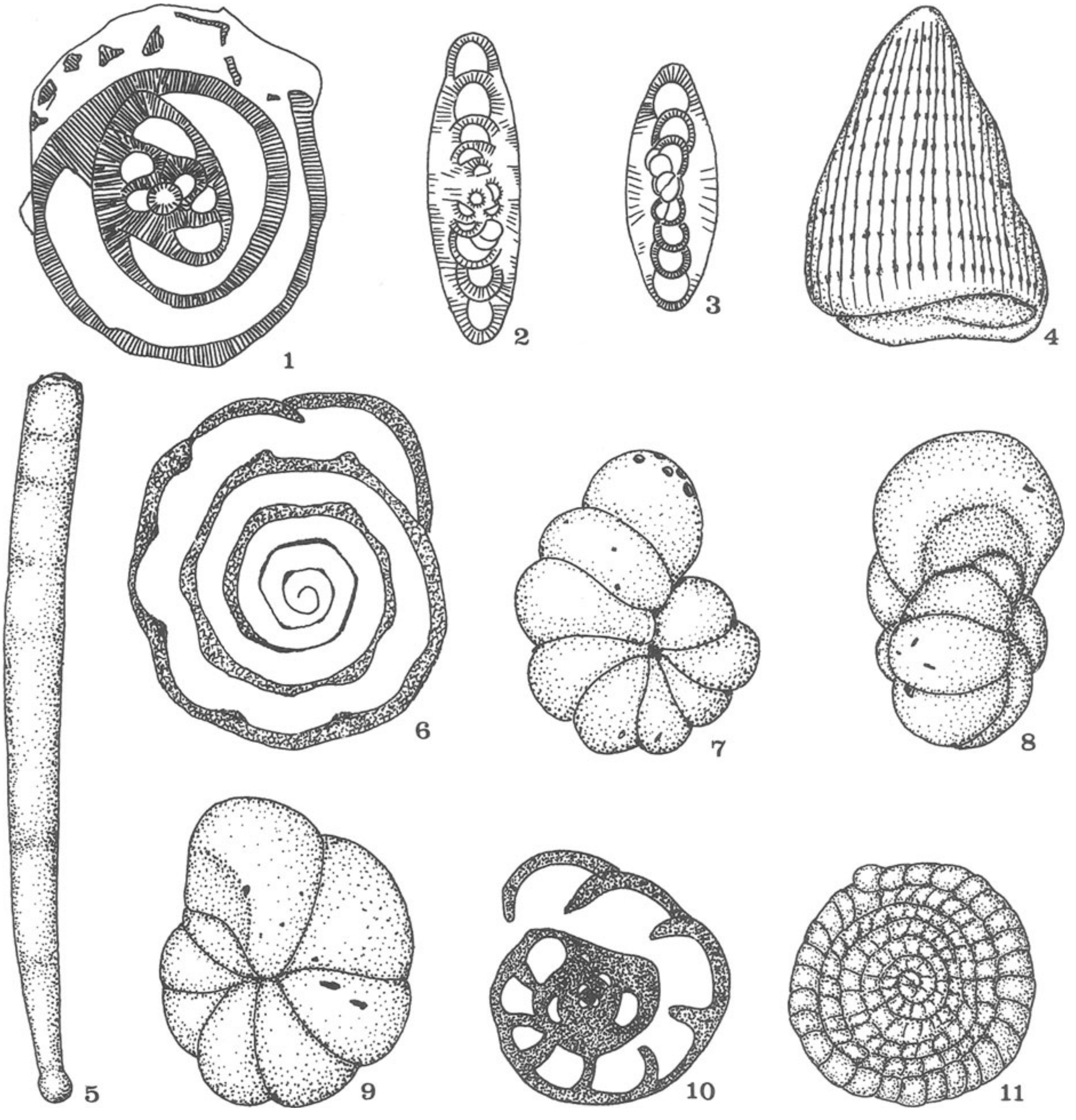
MAIN FAMILIES AND IMPORTANT GENERA OF FUSULINIDA

FUSULINIDA	wall microgranular without optical alignment or with outer hyaline layer; U. Palaeoz. Key figures 7.6, 7.7 and 7.8.
FUSULININA	wall microgranular; U. Pal. Key figures, 7.6, 7.7 and 7.8.
PARATHURAMMINACEA	unilocular or with incipient septation; U.Pal. Key figure 7.6.
PARATHURAMMINIDAE	globular or irregular; U. Pal.
Parathurammina	globular, aperture multiple at ends of protuberences; U.Pal. (homeomorph *Thurammina,* see key figure 6.8).
TOURNAYELLIDAE	streptospiral to planispiral and uncoiled, initial end swollen or restricted as proloculus, aperture at end of tube; U.Pal. Key figure 7.6.
Pseudoglomospira	streptospiral; U.Pal. (homeomorph *Glomospira,*see key figure 6.9)
Tournayella (no. 6)	planispiral with incipient septation; U.Pal. (streptospiral initial part = *Brunsiina; Septatournayella* and *Septabrunsiina,* L. Carb. are recognised by the appearance of rudimentary septa in the adult).
EARLANDIIDAE	tubular, aperture terminal; U. Pal.
Earlandia (no. 5)	initial end globular, tube gradually increasing in diameter to apertural end; U. Pal. (incipient septation = *Paratikhinella*).
ENDOTHYRACEA	test multilocular, streptospiral to planispiral with short axis, biserial and uniserial; U. Pal. Key figure 7.6.
ENDOTHYRIDAE	streptospiral to planispiral and uniserial; U. Pal.
Endothyra (nos. 8 – 10)	streptospiral, partially involute with strong chomata; ? U. Dev. Carb. – Perm. (planispiral = *Eoendothyranopsis,* L. Carb; uncoiled = *Endothyranella,* Carb.; cribrate = *Cribrospira,* Visean; perforate = *Endothyranopsis,* L. Carb.).
Loeblichia (no. 11)	planispiral, evolute with many whorls and chambers; Carb. (strong chomata = *Quasiendothyra,* Dev. – Carb.).
Haplophragmella (no. 7)	planispiral to uncoiled, cribrate; Carb.
Bradyina (nos. 17/18)	planispiral with chamberlets and septal pits; Visean – U.Carb. (septal pits = *Glyphostomella*).
PALAEOTEXTULARIIDAE	biserial to uniserial; Carb. – Perm.
Palaeotextularia (nos. 12/13)	biserial, aperture basal; Carb. – L. Perm. (initial coil = *Palaeospiroplectammina,* L. Carb.).
Deckerellina (nos. 14/15)	biserial, aperture basal with additional areal slit; Visean – Namurian.
Cribrostomum (no. 16)	biserial, aperture cribrate; Carb.
Palaeobigenerina (nos. 19/20)	biserial to uniserial, terminal aperture; Visean – Perm.
Climacammina (nos. 21 – 23)	biserial to uniserial, cribrate; Visean – Perm.
Deckerella (nos. 24/25)	biserial to uniserial, aperture a double slit; Visean – Perm.
Cribrogenerina (nos. 26/27)	uniserial, biserial in juvenile of B form, cribrate; Perm.

SEMITEXTULARIIDAE	biserial to uniserial, compressed; Dev.
Semitextularia (nos. 33/34)	biserial to inverted uniserial, with irregular pillars; Dev. (*Pseudopalmula* is biserial throughout).
NODOSINELLIDAE	Uniserial throughout; U. Pal.
Nodosinella (no. 28)	short chambers with straight suture; ? U. Pal. (compressed with inverted chambers = *Frondilina;* ? single granular layer = *Earlandinita,* L. Carb.).
TETRATAXACEA n.superfam.	trochospiral; U. Pal. Key figure 7.6
TETRATAXIDAE	conical to spreading; Carb. – Perm.
Tetrataxis (nos. 31/32)	conical, commonly with four chambers to the whorl, aperture umbilical; Carb. – Perm. (irregularly spreading = *Polytaxis,* vertical partitions = *Valvulinella*).
FUSULINACEA	planispiral discoid to fusiform, typically large with numerous chambers or chambers divided, wall basically three layered (fusulinellid) or two layered and alveolar (schwagerinid); Carb. – Perm. Key figures 7.7 and 7.8.
OZAWAINELLIDAE	small, discoidal to spherical or irregularly elongate and uncoiling, septa plane, chomata and tunnel, wall fusulinellid; Carb. – Perm. Key figure 7.7.
Staffella (no. 1)	subspherical, involute, strong chomata; Lower Carb. – Perm. (angular and umbilicate = *Nankinella,* U. Carb. – Perm.; angular with massive chomata = *Ozawainella,* Perm.; minute, discoid and partially evolute = *Millerella,* Carb.). N.B. The attempt has been made to separate a number of Upper Carb. species from *Staffella* on size and shape alone: minute (<0.5 mm dia.) and compressed = *Eostaffella,* minute and spherical = *Pseudostaffella,* > 1.0 mm and spherical = *Neostaffella.*
Rauserella (no. 2)	discoidal to irregularly subcylindrical, adult whorls coiled at high angle to juvenile; M. Perm. (*Toriyamaia* has few chambers in adult whorls, no. 3).
FUSULINIDAE	globular to elongate fusiform, septa weakly to strongly folded, with tunnel and chomata, typically with three-layered wall; U. Carb. – Perm. (Subfamily Schubertellinae includes minute irregular and ellipsoidal genera with later coiling at an angle to the initial whorls.)
Fusulinella (no. 4)	polar fluting only, massive chomata; U. Carb. (*Pseudofusulinella* has axial deposits).
Wedekindellina (no. 5)	septa almost plane, massive axial fillings and chomata; U. Carb. (chomata extending almost to chamber ends = *Yangchienia,* M. Perm.).
Fusulina (no. 6)	septa strongly and regularly folded; U. Carb. (wall of single layer = *Palaeofusulina,* U. Perm.).
SCHWAGERINIDAE	large, fusiform to irregularly cylindrical, wall alveolar, septa moderately to strongly folded, typically with single tunnel and chomata; U. Carb. – M. Perm.

Triticites (no. 7)	septa weakly folded over equator, strong chomata; U. Carb. – L. Perm.
Schwagerina (no. 8)	fusiform to subcylindrical with septa strongly folded throughout; L. Perm (inflated outer whorls = *Pseudoschwagerina;* very large and elongate with intense folding = *Parafusulina*).
VERBEEKINIDAE	subspherical to fusiform or elongate-ellipsoidal, septa plane, wall alveolar or single layer, foramina and parachomata throughout in advanced genera; Mid. Perm. Key figure 7.8.
Eoverbeekina (no. 1)	tunnel in early whorls, foramina throughout length in outer whorls with rudimentary parachomata; lowermost M. Perm. – U. Perm.
Verbeekina (no. 2)	spherical, foramina throughout length, parachomata not continous across mid-chamber floor; M. Perm.
Pseudodoliolina (no. 3)	bluntly cylindrical with thin wall and reduced keriotheca, high continous parachomata; M. Perm.
Misellina (nos. 4/5)	ellipsoidal with thick keriotheca and high 'saddle-shaped' parachomata; lowermost M. Perm.
NEOSCHWAGERINIDAE	fusiform to ellipsoidal, septa plane, wall alveolar or single layer, foramina throughout test, parachomata high, spiral septula in all genera plus axial in some, secondary spiral septula in advanced genera; M. Perm.
Cancellina (nos. 6/7)	wall thick, primary spiral septula only, broad parachomata; lowermost M. Perm.
Neoschwagerina (nos. 8/9)	primary septula joining parachomata near septum and up to 3 axial septula per chamber; middle M. Perm.
Yabeina (no. 10)	up to 3 secondary spiral septula in outer whorls and 9 axial septula per chamber; uppermost Middle Perm. (*Sumatrina* has a dense wall, ? single layer, and up to 4 secondary spiral septula; *Lepidolina* is very large with thin irregular primary spiral septula and up to 2 secondary spiral septula).
ARCHAEDISCINA n.suborder	wall with outer, radial hyaline layer; U. Pal. Key figure 7.6.
ARCHAEDISCACEA n.superfam.	test unilocular, streptospiral to planispiral and conical, aperture at end; Carb. – Perm.
ARCHAEDISCIDAE	streptospiral to planispiral; Carb. – Perm.
Archaediscus (nos. 1 – 3)	streptospiral with thickened wall; Carb. – Perm. (planispiral = *Permodiscus*).
LASIODISCIDAE	planispiral to conical with umbilical fillings and septal bridge; Carb. – Perm.
Howchinia (no. 4)	conical with umbilical filling and septal bridges; Carb. (planispiral with tubular extensions = *Lasiodiscus,* U. Carb. – Perm.).
COLANIELLACEA n.superfam.	uniserial chambers, strongly overlapping with partitions in advanced forms; U. Pal.
LUNUCAMMINIDAE	compressed chambers, arched to strongly overlapping; U. Pal.

Lunucammina (nos. 29/30)	arched chambers with median depression; U. Pal. (strongly overlapping and thickened = *Pachyphloia,* U. Perm.).
COLANIELLIDAE	chambers strongly overlapping with partitions; U. Pal.
Colaniella (nos. 35/36)	subfusiform with vertical partitions; U. Perm. (less overlapping and partitions restricted to marginal zone = *Multiseptida,* U. Dev.).

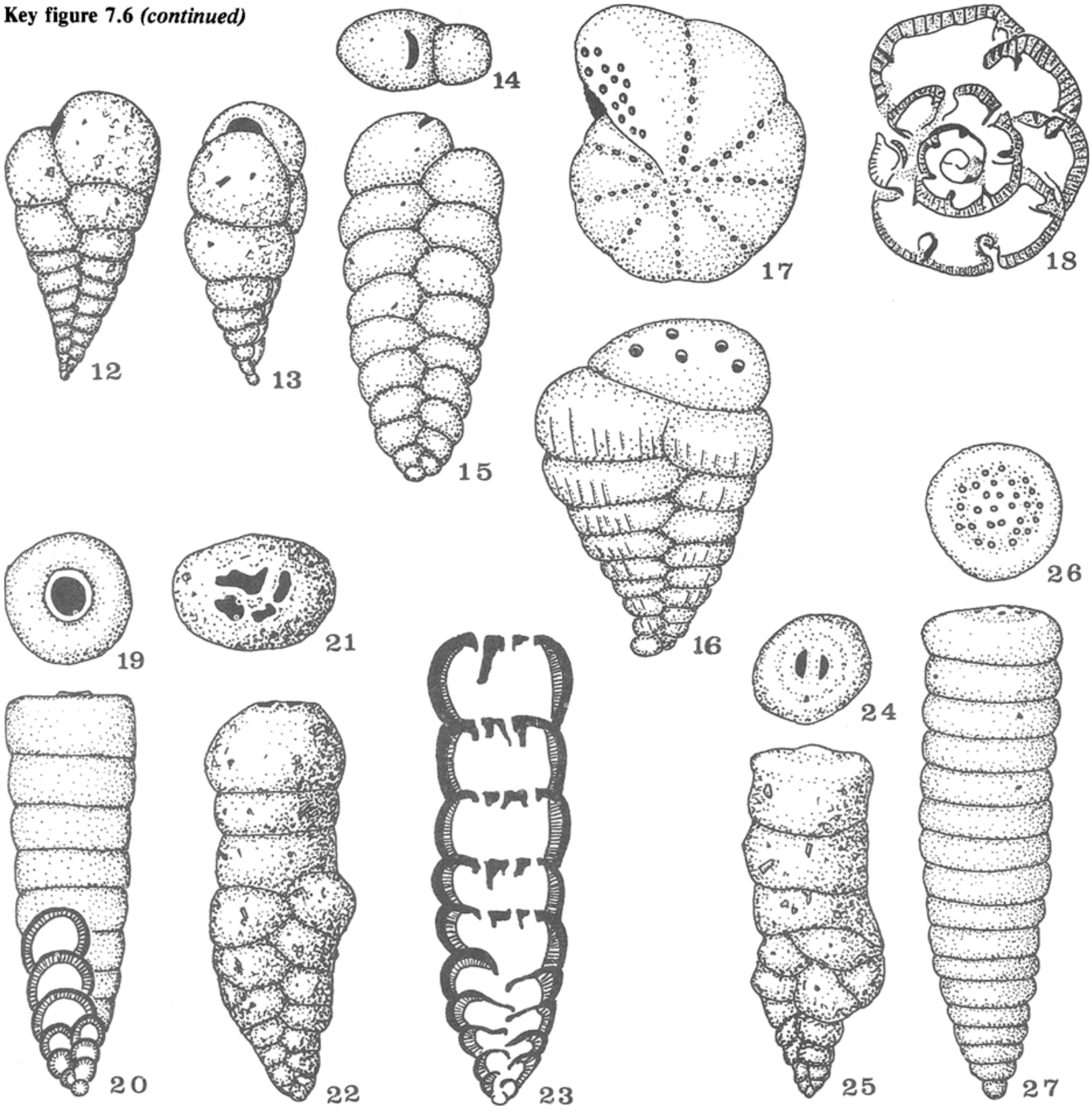


Key figure 7.6 Archaediscacea, Parathuramminacea, Endothyracea, Tetrataxacea, Colaniellacea

1/2 *Archaediscus karreri* **Brady, median and axial sections, after Loeblich & Tappan, × 64**
3 *A. ulmeri* **(Mikhaylov), axial section, × 80**
4 *Howchinia bradyana* **(Howchin), side view, after Loeblich & Tappan, × 105**
5 *Earlandia perparva* **Plummer, side view, after Loeblich & Tappan, × 90**
6 *Tournayella spectabilis* **(Dain), median section, × 60**
7 *Haplophragmella panderi* **(Möller), side view, × 44**
8–10 *Endothyra bowmani* **sensu Brady, peripheral and side views and median section, × 80; 10, × 64**
11 *Loeblichia ammonoides* **(Brady), side view, × 64**

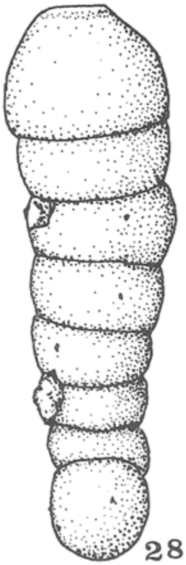
(continued overleaf)

Key figure 7.6 *(continued)*



12/13	*Palaeotextularia grahamensis* (Cushman & Waters), side and peripheral views, × 50
14/15	*Deckerellina istiensis* Reytlinger, after Cummings, apertural and side views, × 50 approx.
16	*Cribrostomum textulariforme* Möller, side view, after Loeblich & Tappan, × 22
17/18	*Bradyina rotula* (Eichwald), side view and median section, × 14
19/20	*Palaeobigenerina geyeri* (Schellwien), apertural and side views, × 14
21/22	*Climacammina cylindrica* (Cushman & Waters), apertural and side views, × 26
23	*C. antiqua* (Brady), vertical section, after Cummings (diagrammatic)
24/25	*Deckerella clavata* Cushman & Waters, apertural and side views, after Loeblich & Tappan, × 30
26/27	*Cribrogenerina sumatrana* Volz, apertural and side views, after Cummings (diagrammatic)

Key figure 7.6 *(continued)*



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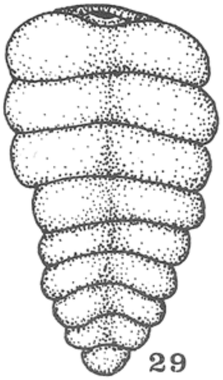

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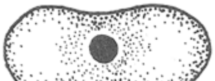

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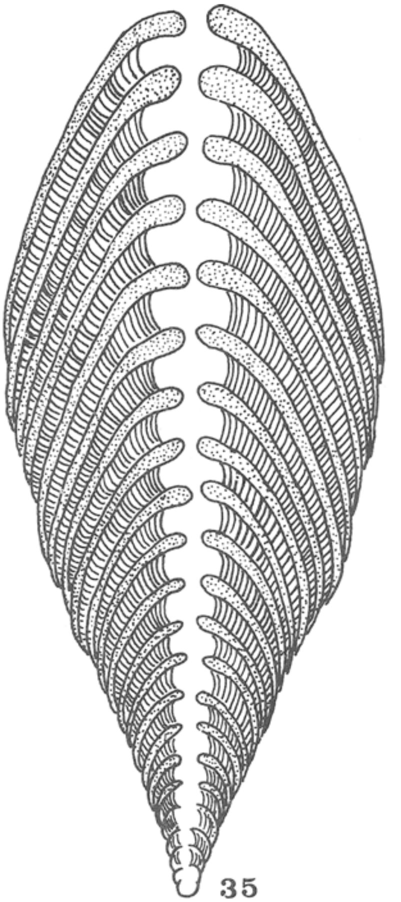

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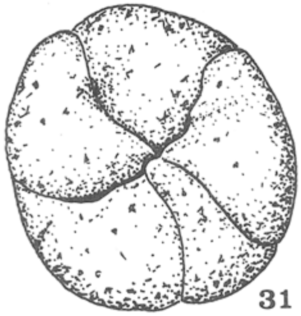

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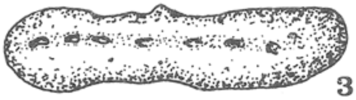

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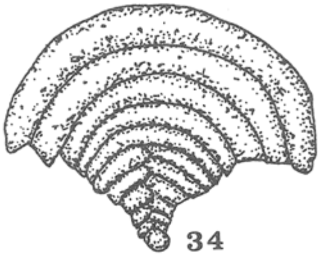

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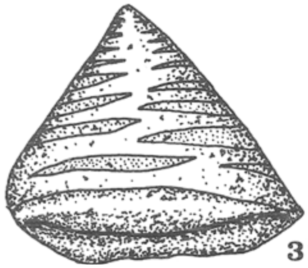

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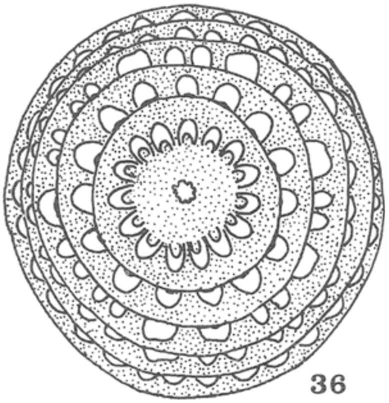

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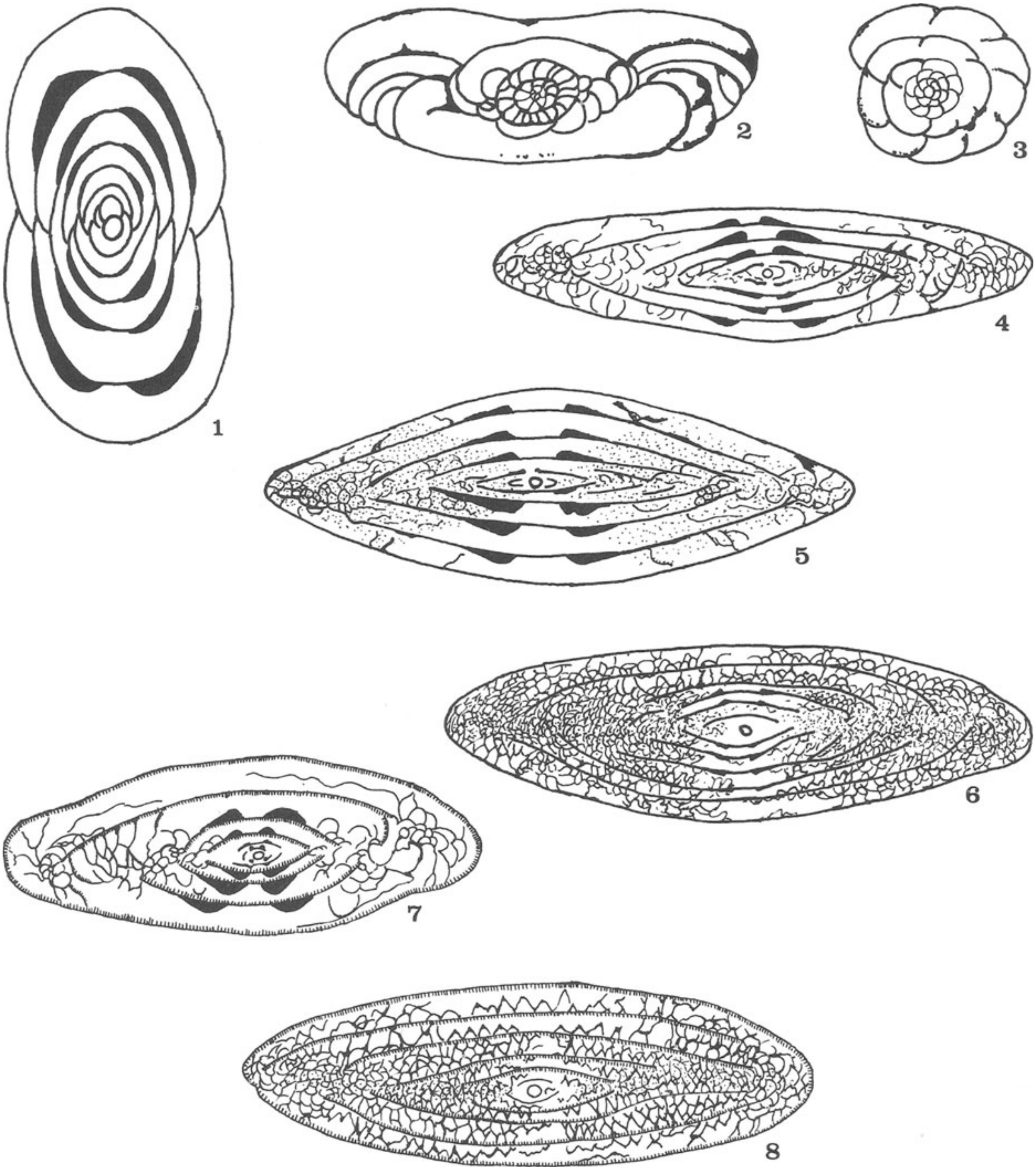
28 *Nodosinella digitata* **Brady, side view, after Loeblich & Tappan, × 48**

29/30 *Lunucammina permiana* **Spandel, side and apertural views, after Loeblich & Tappan, × 105**

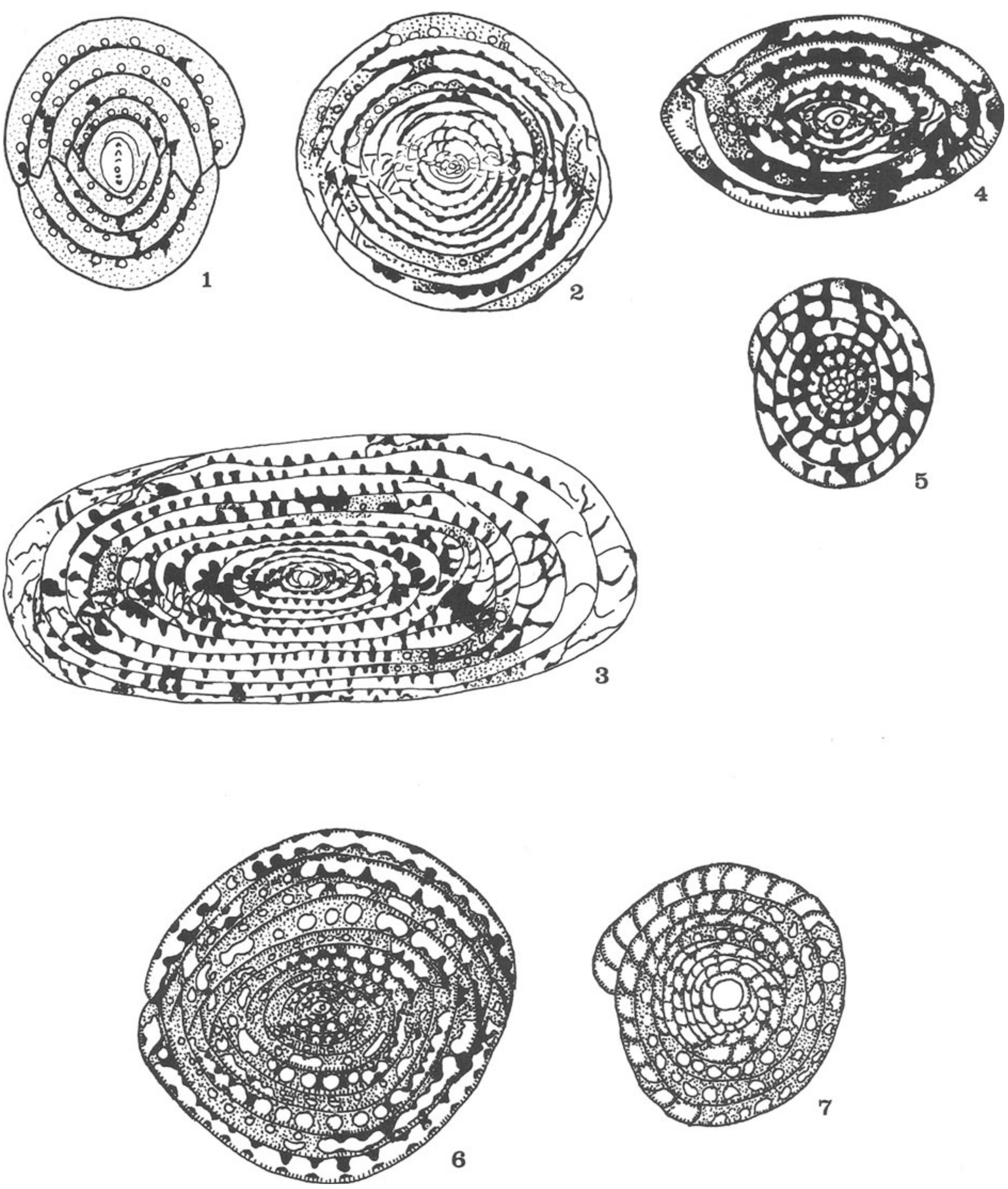
31/32 *Tetrataxis conica* **Ehrenberg, ventral and dorsal views, after Loeblich & Tappan, × 50**

33/34 *Semitextularia thomasi* **Miller & Carmer, apertural and side views, after Loeblich & Tappan, × 86**

35/36 *Colaniella parva* **(Colani), vertical and horizontal sections, after Loeblich & Tappan, × 100**



Key figure 7.7 **Ozawainellidae, Fusulinidae, Schwagerinidae**
1 ***Staffella expansa*** **Thompson, axial section, × 50**
2 ***Rauserella erratica*** **Dunbar, axial section, × 25**
3 ***Toriyamaia laxiseptata*** **Kosaki, median section, × 25**
4 ***Fusulinella juncea*** **Thompson, axial section, × 20**
5 ***Wedekindellina matura*** **Thompson, axial section, × 30**
6 ***Fusulina mysticensis*** **Thompson, axial section, × 10**
7 ***Triticites milleri*** **Thompson, axial section, × 20**
8 ***Schwagerina huecaensis*** **Dunbar & Skinner, axial section, × 10**

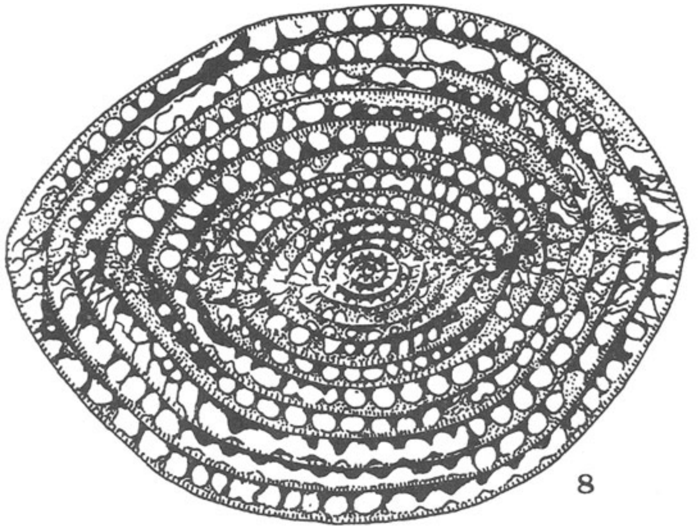


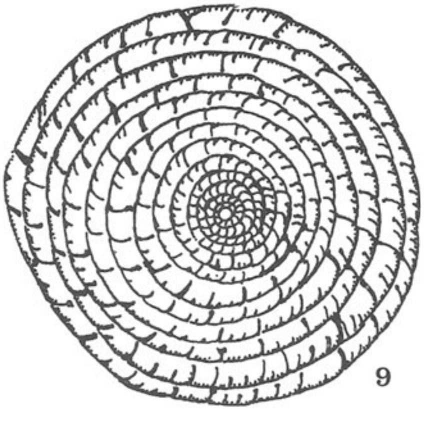
Key figure 7.8 Verbeekinidae, Neoschwagerinidae

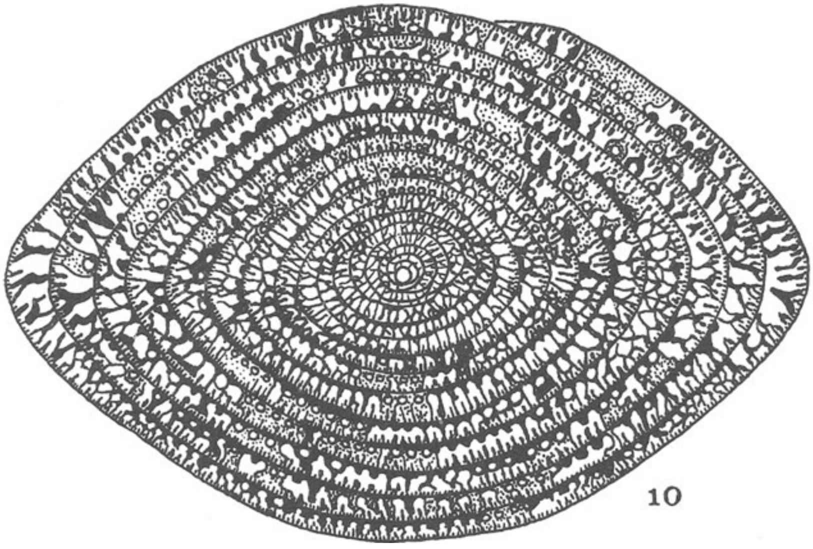
1 ***Eoverbeekina intermedia*** **Lee, axial section × 12**
2 ***Verbeekina karinae*** **(Miklukho-Maklay), axial section, × 12**
3 ***Pseudodoliolina ozawai*** **(Deprat), axial section, × 20**
4/5 ***Misellina ovalis*** **(Deprat), axial and median sections, × 15**
6/7 ***Cancellina primigera*** **(Hayden), axial and median sections, × 20**

(continued overleaf)

Key figure 7.8 *(continued)*







8 *Neoschwagerina haydeni* **(Dutkevich & Khabaka), axial section, × 20**
9 *Neoschwagerina gifuensis* **(Honjo), median section, × 15**
10 *Yabeina globosa* **(Yabe), oblique axial section, × 10**

Chapter 8

The Miliolida

> ... though both by inclination and teaching experience I am a 'lumper', I have found it necessary to retain these generic divisions (in the Ophthalmidiidae). They seem to have significance in the pattern of evolution within the group, and though the trends are only dimly visible they will become clearer with the years if the individual threads are separated.
>
> (Wood to Macfadyen, 1946)*

The end of the Palaeozoic and the beginning of the Mesozoic were times of great faunal change and renewal, illustrated very well by changes in the Foraminifera. The large fusulinaceans became extinct during the final stage of the Permian and by the end of the period all the other members of the order (apart from some problematical endothyrids) apparently disappeared, being replaced during the early Mesozoic by porcelaneous and hyaline groups.

Simple porcelaneous genera appeared during the Upper Palaeozoic and played an important role in reefal communities (Henbest, 1963) but remained subordinate to the Fusulinida. From the Triassic onwards abundance and diversity markedly increased to make this order one of the most important in the Foraminifera. They are particularly useful in stratigraphical studies because they range down to the present day and dominate shallow, warm water, microfaunal assemblages. This means that the ecology of living species can be examined in detail and the results applied to problems of palaeogeography. Study of this group is especially rewarding in that it includes the majority of living Larger Foraminifera which are a key to the understanding of the ecology and relationships of similar, extinct forms.

Like the Fusulinida, the Miliolida are important contributors to lithology and are rock-formers from the Jurassic onwards, but with spectacular examples in the Upper Cretaceous and Palaeogene when the alveolines proliferated in mid-latitudes. This group resemble the planispiral-fusiform fusulinaceans and attain even larger sizes, up to 10 cm length.

Although planispiral coiling is common, the dominant mode is a unique style of winding growth with the aperture alternating from end to end of the test. A bilocular juvenarium is a characteristic feature of the higher families, with a protoconch followed by a tubular deuteroconch that may consist of several planispiral whorls but tends to be reduced to half a turn and may be narrowed (flexostyle). The tendency to a geometric form with biform and even triform growth lends itself to evolutionary studies and has led to classic contributions to the debate on recapitulation versus proterogenesis in Foraminifera (see chapter 4 and Wood and Barnard, 1946).

As discussed previously, the Miliolida are also distinguished by a unique wall structure with a basic layer of calcite laths in random array and generally with inner and outer veneers of tabular crystals (rhombohedra). In transmitted light a rich brown coloration is produced by included organic matter. We have seen (chapter 5) how the apparent lack of perforations came to be considered an important character in classification and how the discovery of pores in the proloculus of *Peneroplis* undermined this idea and devalued wall structure at the same time.

More recently, studies by TEM (Lynts and Pfister, 1967) and SEM (Bignot *et al.*, 1971) have revealed pits in the outer walls of genera such as *Miliolinella, Archaias, Peneroplis* and *Spirolina* which end blindly in the random inner layer (pseudopores). In addition, Bignot *et al.* describe irregular tubules in *Peneroplis* which may connect with the pits.

A final blow to the idea of the absence of pores in the Miliolida would appear to have been dealt by their discovery in the new Triassic, quinqueloculine genus *Miliolipora* (Brönnimann and Zaninetti, 1971). However, caution is necessary. The 'pores' in *Miliolipora* are highly irregular in orientation and distribution and many are blind. Similarly, the tubules illustrated in *Peneroplis* are, again, both irregular and unevenly distributed. It is difficult to avoid the suspicion that they may have been produced by boring organisms which commonly attack tests in death assemblages, especially where sedimentation is slow. This points up the problem of the interpretation of the new structures now being revealed by electron microscopy and the necessity of further work before radical departures are made in classification and phylogeny.

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*See discussion following Wood and Barnard (1946).

CHAMBER FORM AND COILING MODES

The Miliolida are the third largest of the orders of Foraminifera and during their long evolutionary history since the Upper Palaeozoic have shown considerable diversity. As shown by the table of coiling modes (figure 4.3), the dominant form of chamber arrangement is winding (33 per cent of the total genera), characteristically with two elongate chambers in each whorl arranged in a stable geometric pattern. This is followed by planispiral to uncoiled arrangement (27 per cent), the two modes together making up more than half of the total. Less abundant but characteristic of certain groups and highly successful at the species level are planispiral-fusiform (9 per cent) and annular-discoid arrangement (8 per cent). Other modes are rare, particularly trochoid arrangement, when the Barkerinidae are excluded, as by Hamaoui (1973) and Hamaoui and Saint-Marc (1970). A feature of the order is the relatively high percentage of unilocular/bilocular genera and attached, usually irregular, genera.

The superfamilies and families are distinguished by these differences in coiling modes together with differences in aperture form. As in the case of the lituolids, groups showing parallel development in chambering can often be separated on the basis of tooth structure. In addition, advanced forms show the development of partitions and chamberlets along a number of lines.

Nubeculariacea

Bilocular genera which consist of proloculus and long tubular second chamber only, family Cornuspiridae, and genera in which a cornuspirid juvenarium is followed by irregularly sized chambers, family Nubeculariidae, are placed in the superfamily Nubeculariacea. The Fischerinidae are therefore combined with the Nubeculariidae, as by Anglada and Randrianasola (1972). The aperture is usually formed by the open end of the tube but may be a compressed slit. Many of the genera in both families are attached and the uncoiled forms are irregular in habit. As an attached mode of life has probably developed many times, this feature is not thought to be of family or subfamily significance.

Ophthalmidiacea

Genera in which a cornuspirid juvenarium is followed by elongate, tubular chambers and the aperture is simple, are included in the superfamily Ophthalmidiacea. The family Palaeomiliolinidae includes genera in which the adult chambers are regularly two per whorl and arranged in various planes. Planispiral genera in which the chambers are separated by a plate-like flange and the length decreases from more than one whorl to less than half a whorl length are included in the family Ophthalmidiidae. Zaninetti & Brönniman (1969) emended *Ophthalmidium* to include all other related genera. This view is not followed here but rather that of Wood and Barnard (1946) who found it necessary to retain these generic divisions, 'after a careful comparison of the Lias species with Recent representatives'. See also Copestake (1978). This family includes the advanced annular-discoid form *Discospirina* with partial partitions. It is distinguished from similar annular-discoid members of the Soritacea by its *Haurinella*-like early whorls. As it is the only genus known, occurring late in geological time, Neogene to Recent, and apparently clearly indicates its origin by the form of the juvenile, it is retained with the Ophthalmidiacea, subfamily Discospirininae, Wiesner (1931).

Soritacea

Genera that are close-coiled, planispiral to uniserial, flabelliform or annular-discoid, tending to develop incomplete partitions or chamberlets, with multiple apertures, are included in the superfamily Soritacea. This superfamily includes several families of uncertain affinity. In particular the relationship between the Mesozoic and Tertiary group is obscure.

The Tertiary family, Soritidae, includes planispiral to evolute, annular discoid genera, the later forms showing a considerable increase in size. *Amphisorus* shows the partial development of a double tier of chamberlets. In *Marginopora,* in which the test is a biconcave disc up to 1 cm diameter with a porous margin of multiple apertures, a third layer is intercalated to give a tripartite structure. The Upper Cretaceous Meandropsinidae closely parallel the Soritidae in structure and reach even larger sizes. Characteristically the genera in this family are involute with incomplete partitions. Here, rather than a single layer becoming divided into several tiers of chamberlets, the numerous overlapping chambers produce the appearance of a layered structure in vertical section. In *Meandropsina* in particular, the outer annulae may become meandrine. However, evolute genera also occur and *Broeckina* closely resembles *Cyclorbiculina,* being almost a complete homeomorph of it, apart from its incomplete partitions.

Genera which become uncoiled and cylindrical or compressed and flabelliform in the adult, again with incomplete partitions, are included in the *Praerhapydioninidae.* A number of genera formerly associated with this group, such as *Rhapydionina* and *Rhipidionina* (Sen. – Maas.), are distinguished by the presence of a canaliculate central columella and together with their allies, *Pseudedomia* and *Murciella,* are transferred by Hamaoui and Fourcade (1973) to the Alveolinidae (Miliolacea herein — see the Summary Classification at the end of the chapter).

Miliolacea

This superfamily includes forms with elongate chambers wound in various planes with dentate aperture, family Miliolidae, the characteristically planispiral-fusiform Alveolinidae and the planispiral to cylindrical, or flabelliform, Rhapidioninidae.

The basic coiling mode in the Miliolidae is illustrated in figures 8.1, 8.2 and 8.3. In *Quinqueloculina* (figure 8.1B) the chambers are added at about 144° to each other to give a test with five chambers visible externally (quinqueloculine), with adjacent chambers at about 72° to each other. As a consequence of this mode of growth the aperture alternates from end to end of the test and as several sets are usually developed (five chambers in each) the early chambers are entirely hidden and can only be studied in thin section.

In *Triloculina* (figure 8.1C) the final chambers are added at about 120° to each other and only three are visible externally. In this genus the microspheric generation normally shows a quinqueloculine or subquinqueloculine initial part.

As shown by figure 8.2, even in specimens near to the holotype of *Quinqueloculina, Q. ex gr. seminulum,* the test may appear externally quadriloculine due to the final chambers being added at an angle slightly over 150° and with a greater amount of overlap. Twisting of the axis up to 90° may occur in the early whorls of some species so that again only four, or even three, chambers are visible externally — the 'kryptoquinqueloculine' structure of Bogdanovich (1969) and Luczkowska (1972). Similar irregularities may affect triloculine species (pseudotriloculine structure) and, indeed, it appears that it is only in the 'classic' triangular and trigonal species of *Triloculina* that the final chambers are added regularly at about 120°, aided apparently by the geometric shape, and there is usually a variation of some 20° either side. These irregularities are well shown in the quinqueloculine to triloculine genus *Miliolinella* (figure 8.1, D1 and D2). Although both flattened quinqueloculine and triloculine tests are achieved, the angle of chamber addition is fairly constant between 140° and 150°. Ponder (1974) gives a rapid method of measuring the angles of the chambers of such difficult forms in apertural view by means of a transparent overlay. Care must be taken in the interpretation of the angles and, normally, thin sections will be required to reveal changes with growth.

Increase in the angle between successive chambers to 180° leads to forms which are evolute, bilocular-planispiral in the final whorls, such as *Massilina* (figure 8.2) and to *Spiroloculina* in which the quinqueloculine initial part is reduced and may be absent in the A forms of some species. In contrast, involute, bilocular structure is shown in *Biloculina* and *Pyrgo* (figure 8.1, F1 and F2) in which only the last two chambers are visible externally. Complete overlapping, to achieve a test that appears unilocular in external view, occurs in genera such as *Idalina* (figure 8.1G). In contrast to the trend towards increasing involution, some forms pass from quinqueloculine to planispiral, as in *Hauerina,* and to uncoiled uniserial, as in *Raadshoovenia.* In *Sigmoilina* the chambers are sigmoid, rather than quinqueloculine.

Besides these interesting variations in 'milioline' winding the family shows great diversity in aperture shape and tooth structure (figure 8.1A and plate 10). So much so, that the tendency of earlier workers was to lump the different kinds

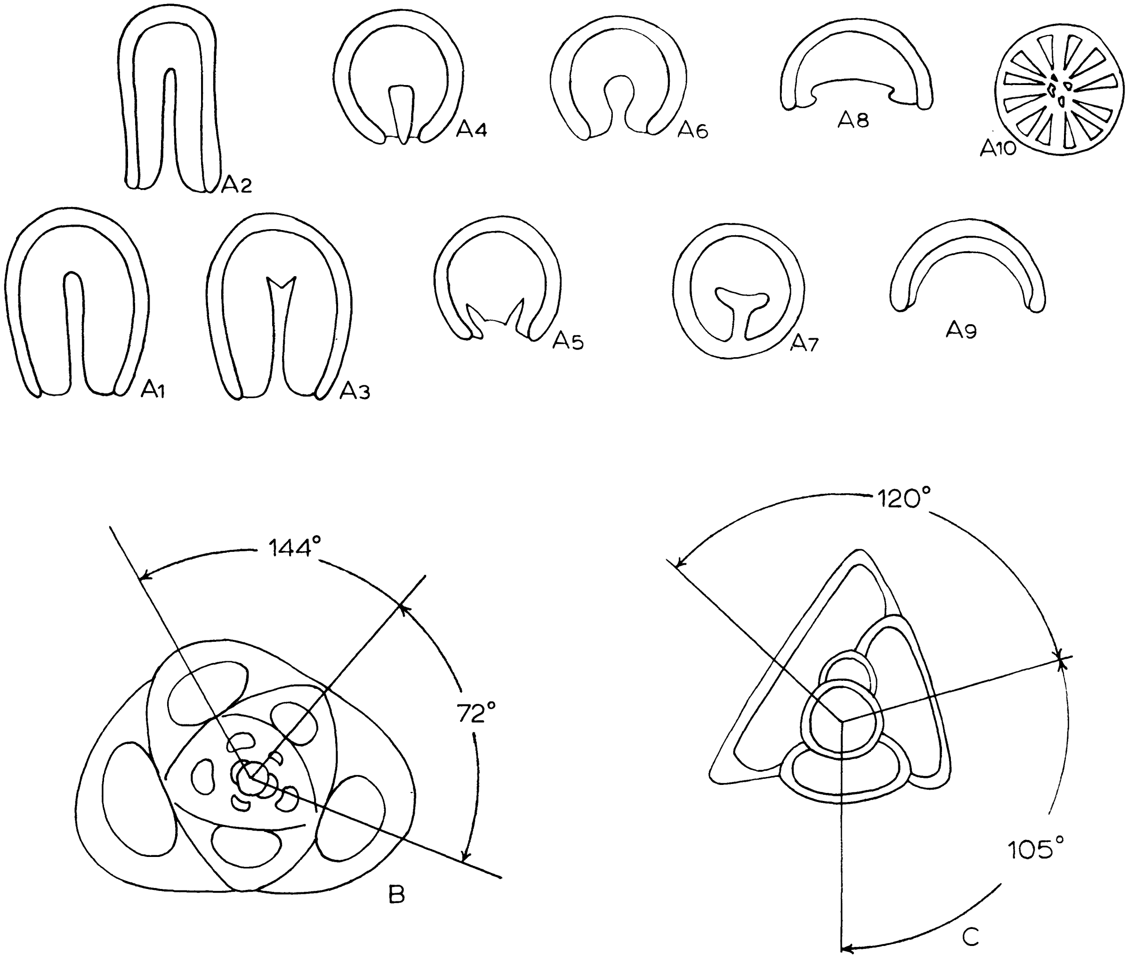


Figure 8.1 Chamber arrangement and dentition in the Miliolidae

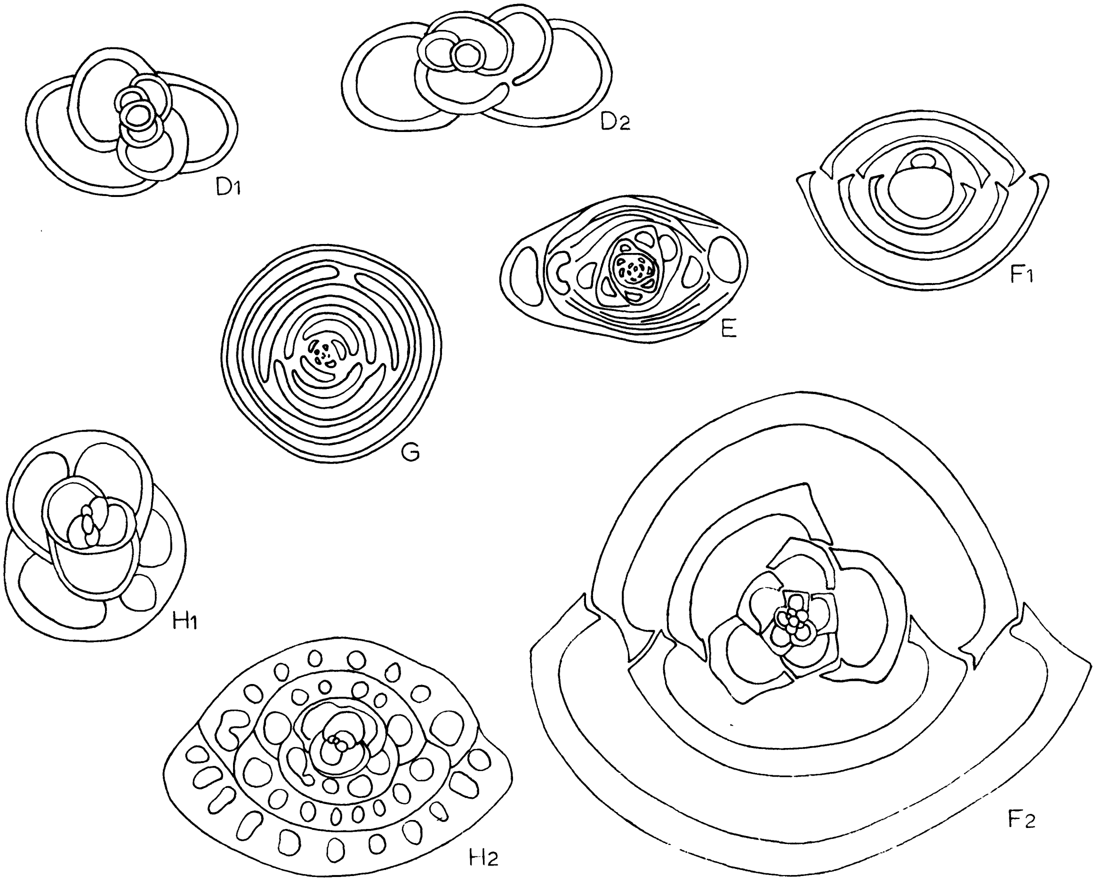
A Variation in tooth structures:

A1 oval with simple bar
A2 compressed with simple bar = *'Lachlanella'* type
A3 oval and bar minutely bifid = peg-like
A4 circular and tooth wedge-shaped
A5 circular and reduced, bifid tooth
A6 circular and tooth spoon-shaped
A7 circular with T-shaped, bifid tooth
A8 semicircular with reduced subrectangular tooth
A9 semicircular with broad, flap-like toothplate
A10 round with complex trematophore

B Horizontal section to show chamber arrangement in *Quinqueloculina seminulum*, showing successive chambers added at about 140° to each other resulting in 5 chambers at the periphery with an angle of about 72° between adjacent ones

C Horizontal section to show chamber arrangement in *Triloculina neudorfensis* (after Luczkowska), penultimate chamber added at about 105° to the third from last chamber and the final chamber at about 120° to the penultimate one

Figure 8.1 *(continued)*



D Horizontal sections to show variation in chamber arrangement in *Miliolinella banatiana* (after Luczkowska)

D1 triloculine to quadriloculine form

D2 flattened triloculine to quinqueloculine form with twisted coiling axis. Note that most chambers are added successively at between 140° and 150°

E Horizontal section to show quinqueloculine to sigmoid chamber arrangement in *Sigmoilina sigmoidea* (after L. & T.)

F Horizontal sections to show chamber arrangement in *Pyrgo sarsi* (after Schlumberger)

F1 A form, bilocular throughout

F2 B form, with quinqueloculine and triloculine juvenile chambers. Note triloculine chambers are added at about 140° to each other ('pseudotriloculine')

G Horizontal section to show quinqueloculine, to triloculine, to biloculine, to single overlapping chambers in the B form of *Idalina antiqua* (after L. & T.)

H Horizontal sections to show quinqueloculine, to triloculine, to biloculine chamber arrangement in *Fabularia howchini* (after Schlumberger)

H1 enlargement of juvenile part showing that the triloculine chambers are added at 140°

H2 adult chambers with vertical tubular chamberlets

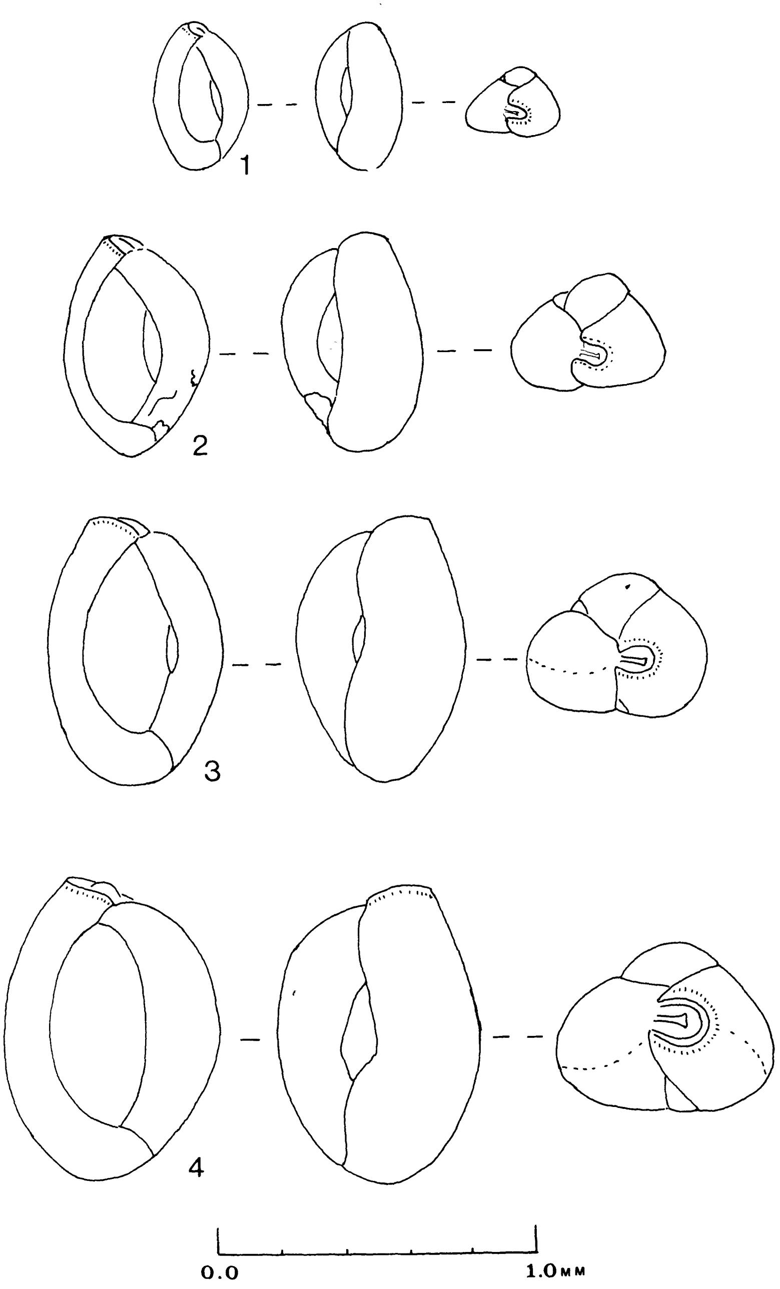
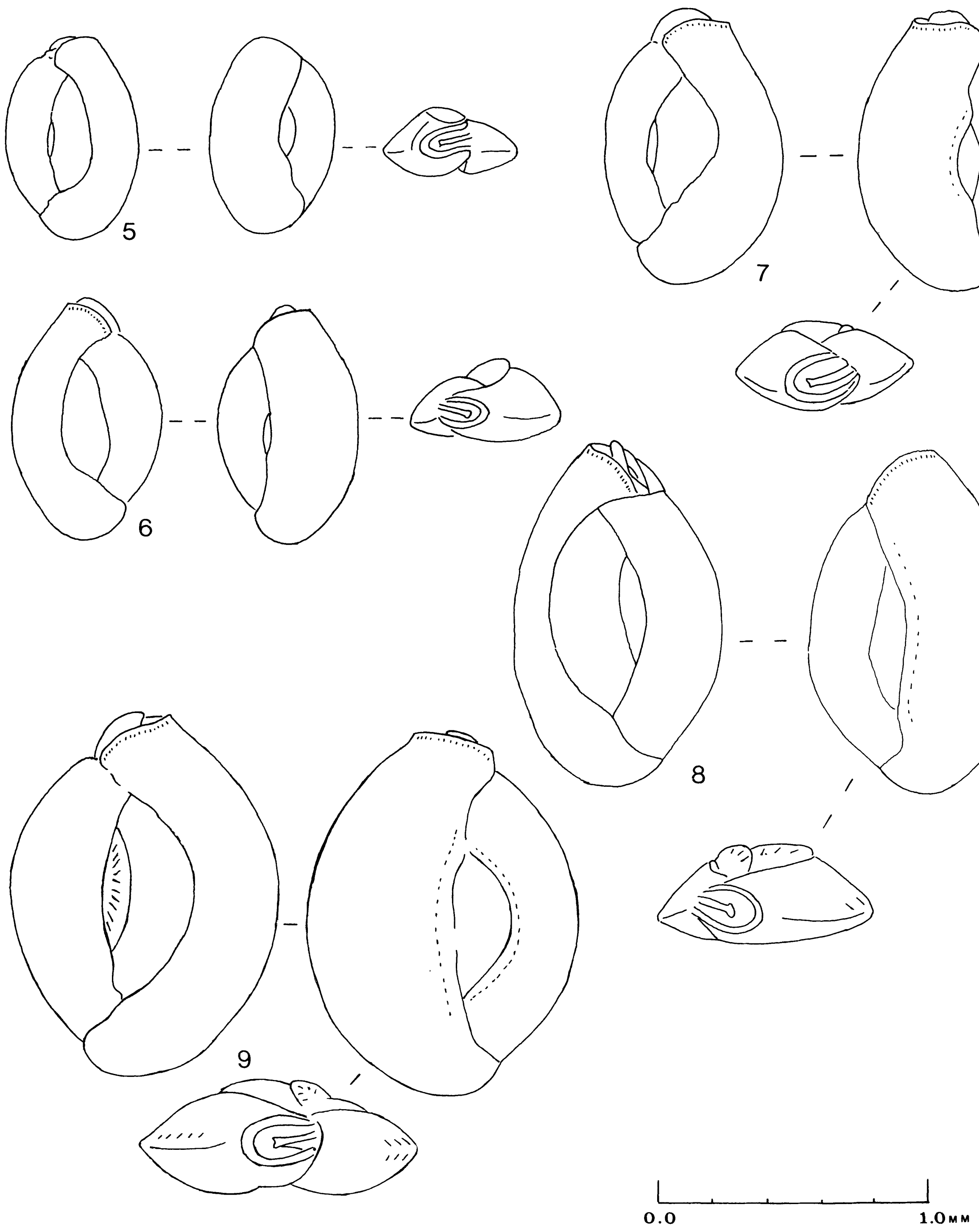


Figure 8.2 Growth series in *Quinqueloculina* and *Massilina*. 1 – 4 *Q. seminulum orbicularis*;



5–9 *M. secans* **var. See also figure 8.3, no. 12. All specimens from Cardigan Bay**

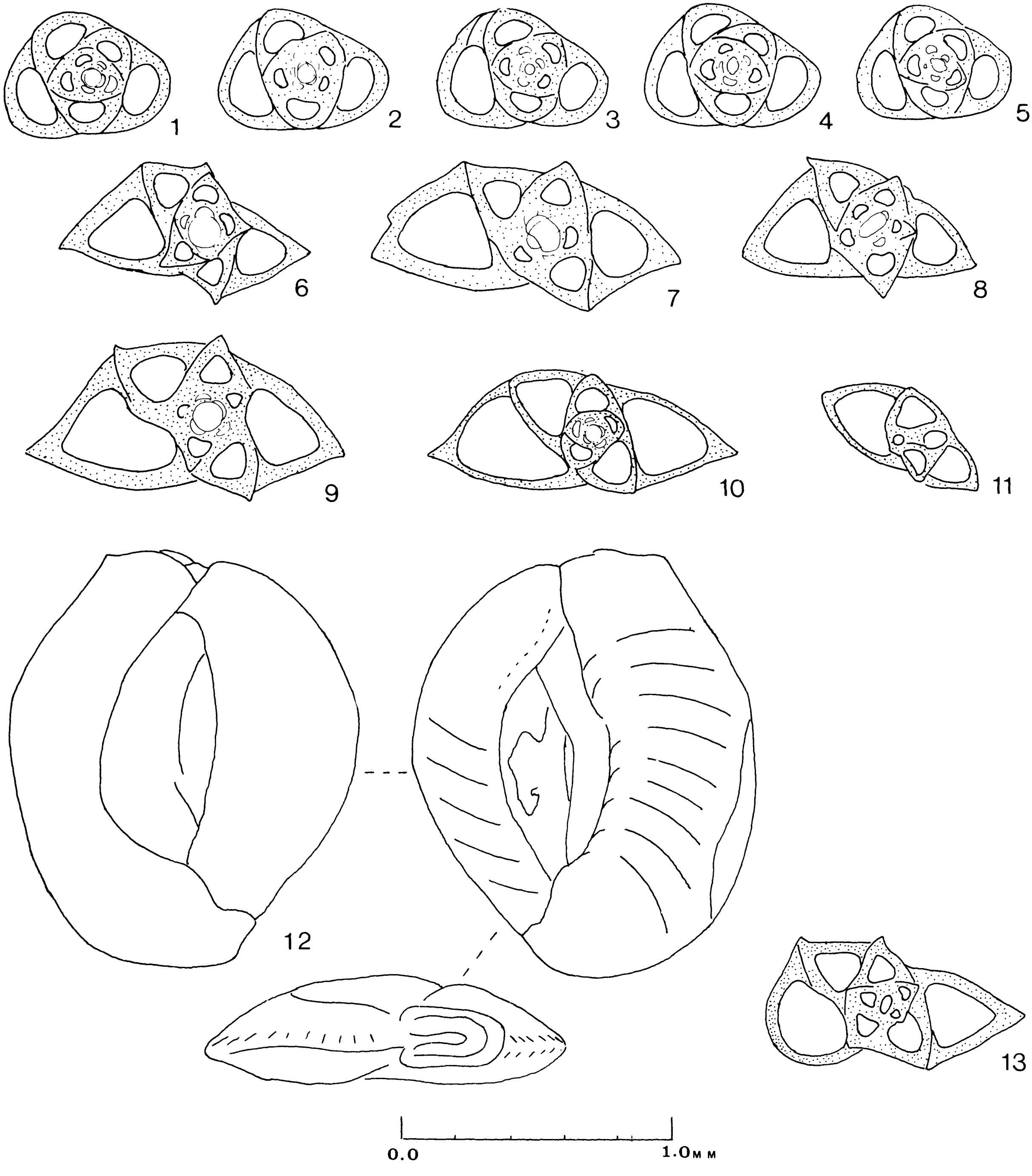


Figure 8.3 Comparison between horizontal sections of *Quinqueloculina* and *Massilina*. 1–5 *Q. ex gr. seminulum*; 6–11 and 13 *M. secans*; 12 side view of *M. secans* var. large specimen. Specimens of *M. secans* from East Mediterranean, except no. 12

together under broad groupings based on chamber arrangement and it is only fairly recently, beginning with Wiesner (1931), that systematic attention has been paid to them. They were made the basis of subfamily distinctions in the 'Treatise' of Loeblich and Tappan (1964) and research has been carried further by Vella (1957) and Luczkowska (1972) in discrimination at the generic level. Some of the main variations are shown in figure 8.1, A1 – A10. The relation between aperture form, tooth structure and coiling mode in various groups of Miliolidae is shown in figure 8.4

In the *Quinqueloculina* group the aperture is truncate and oval, or compressed with a bar-like tooth that continues internally a short way and may be incipiently bifid, or on the other hand the aperture is produced and round with short, bifid, wedge-shaped, T-shaped or spoon-shaped tooth. It seems likely that further splitting is required in this group, especially to discriminate species with spoon-shaped or T-shaped teeth.

In the *Miliolinella* group the aperture is semicircular to compressed and the tooth structure either a reduced rectangular plate or a broad flap.

There is also a group including *Cribrolinoides* in which the aperture is irregularly cribrate or of slits or chevrons. These have hitherto not been separately distinguished but seem to stand apart from the *Miliola* group which have definite apertural cover plates or trematophores. Within this latter group are a number of genera, including *Fabularia* with incomplete vertical partitions that have long been distinguished as a separate subfamily, Fabulariinae Ehrenberg (1839).

As is well shown by the chart these groups show most of the main coiling modes and therefore do appear to represent separate lines of development. Indeed, the *Quinqueloculina* group and *Miliolinella* groups clearly show more than one line and probably merit raising to family rank. If the *Miliola* group were raised to family rank the Fabularinae might fall naturally into place as a specialised subfamily. Incidentally, Hamaoui and Fourcade (1973) suggest that the Fabulariinae should be removed, together with the *Rhapydionina* group, to the Alveolinidae. This view is not followed here because of their dominantly bilocular chambering and milioline winding. *Pseudofabularia* Robinson (1974) is bilocular but in all other respects is a planispiral-fusiform alveolinid.

The family Alveolinidae includes genera that are planispiral in the adult part and spherical to fusiform in shape. The basic morphology is shown in figure 8.5. As in the case of the morphologically similar fusulinaceans, identification depends upon axial and equatorial (median) sections.

The juvenarium (embryonic apparatus) consists of a spherical proloculus followed by a spiral tube (flexostyle), succeeded in *Glomalveolina* and in the B forms of *Alveolina* and some other genera by a milioline nepion (pre-adult phase). There are numerous chambers in the adult (ephebic) planispiral part. These chambers are depressed and reach from pole to pole. They are marked on the exterior by septal furrows. The chambers are divided by vertical septula, inserted parallel to the direction of coiling (spiral), into elongate chamberlets which communicate to the exterior via multiple openings in the apertural face, a single opening corresponding to each one. There may also be horizontal partitions dividing the chambers into several tiers of chamberlets, then represented by several rows of openings in the apertural face. Communication through the chambers is maintained by a system of passages through the vertical septula (canals). These may be situated in front of the septum (postseptal) or behind it (preseptal).

The wall is porcelaneous throughout and consists of an external lamina, usually light in colour and an internal, darker basal layer. Thick deposits of secondary calcite (flosculin) may coat the chamber floors, in some cases restricting the chamberlets to a small space in the roof (flosculinisation).

In external appearance the alveolines closely resemble the fusulinaceans, attaining approximately the same range of size and with the septal furrows imparting the characteristic rugby ball appearance to the generally fusiform tests. However, the alveolines differ fundamentally in their imperforate, porcelaneous wall structure and slightly eroded specimens are recognisable by the strongly marked spiral septula. The alveolines also differ markedly in the way in which the chambers are subdivided. Septal folding does not occur and the spiral septula reach the floor across the chamber. In the Fusulinacea, the Neoschwagerinidae are the only group with septula. Here both spiral and axial septula occur but as roof pendants, not reaching the floor in the centre of the chamber. Again, although both groups show a strong tendency towards deposition of secondary calcite, flosculinisation occurs more evenly across the floor of the chamber, rather than being almost entirely concentrated in the axial zone as in the Fusulinacea.

The different genera within the family are determined on the basis of the following characters. In the simplest case the chambers are

Subfamilies	Quinqueloculininae		Miliolinellinae		Cribrolinoidinae n. sub family	Miliolinae	Fabulariinae
aperture tooth / chambers	oval to rectang. long bar, may be bifid at end	round wedge, spoon* or short & bifid	semicircular - compressed, low rectang, may be hooked or rounded	semicircular broad flap	slits or chevrons irregular	round with trematophore partitions absent	incomplete to complete
Quinqueloculine - 'quadriloculine'	*Quinqueloculina* (suppl. teeth = *Podolia*)	*Adelosina*	*Varidentella*	*Scutuloris*	*Cribrolinoides*	*Miliola*	
Quinqueloculine - triloculine (pseudotril oculine)	*Affinetrina*	*Triloculina*		*Miliolinella* (crenulate = *Crenetella*)	*Cruciloculina*		*Austrotrillina* (has alveolar wall)
Quinqueloculine - involute biloculine	*Biloculina*	*Sinuloculina*	*Pyrgo*	*Biloculinella*	*Pyrgoella* chevrons *Cribropyrgo* irregular	*Nevillina*	*Fabularia* depressed = *Lacazina*
Quinqueloculine to completely over-lapping						*Idalina*	*Periloculina* (entirely over-lapping = *Lacazinella*)
Quinqueloculine = evolute biloculine	*Massilina* (dominantly biloculine = Spiroloculina)		*Flintia*	*Riveroina* (has oblique sec. septa)		*Heterillina* (agglut. ext. = *Ammomassilina*)	
Sigmoid		*Sigmoilina* (agglut. ext. = *Sigmoilopsis*)					
Sigmoid - evolute biloculine		*Spirosigmoilina*					
Quinqueloculine - planispiral	*Flintinella*	*Ptychomiliola*		*Nummoloculina*	*Involvohauerina*	*Hauerina*	*Pseudohauerina*

Figure 8.4 Coiling mode and aperture form in genera and subfamilies of the Miliolidae. *May require separate generic status

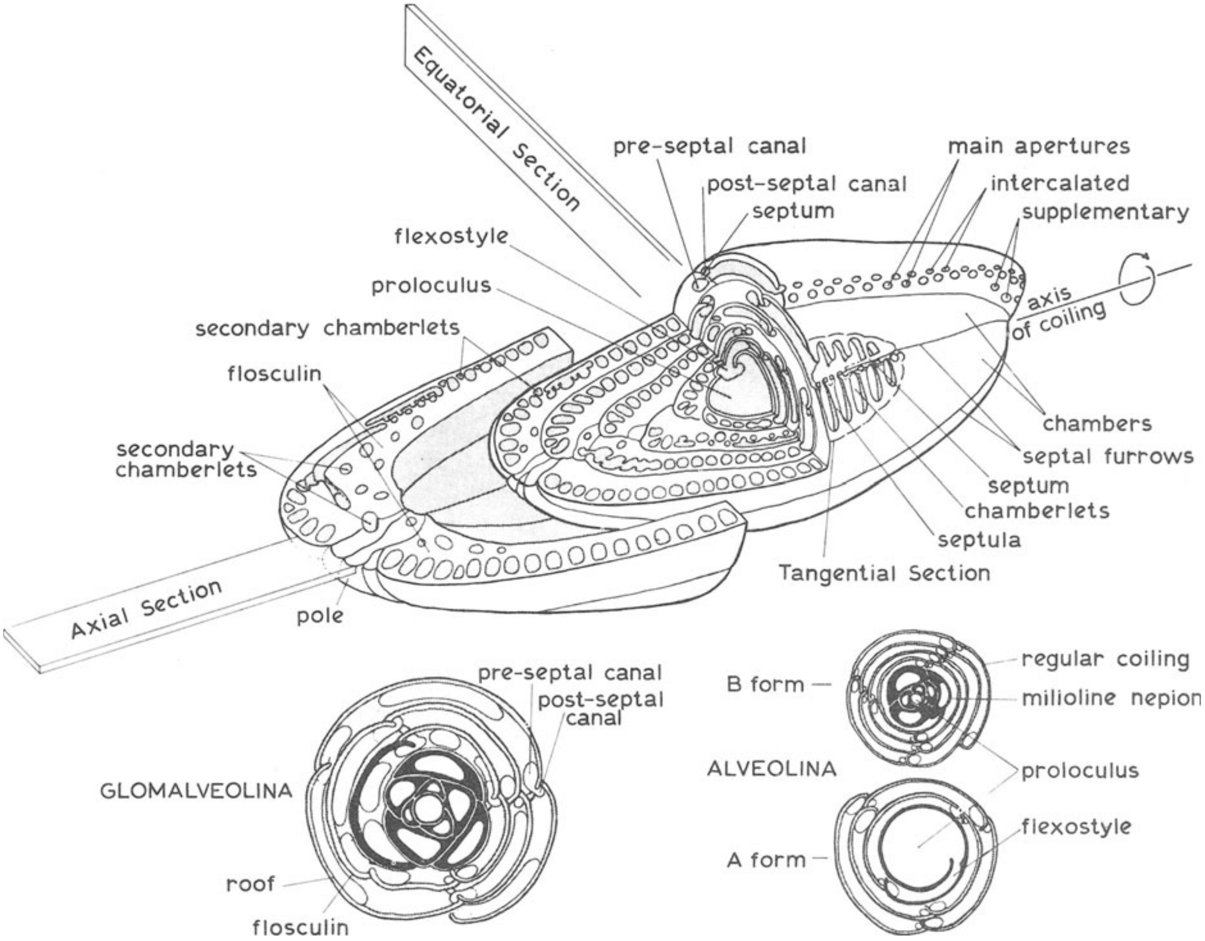


Figure 8.5 Alveolinid morphology and terminology. After Hottinger (1960), ***Mem. Soc. Pal. Suisse*****, 75/76:1 – 243**

subdivided by vertical secondary septa running in the direction of coiling, giving one layer of primary chamberlets as in *Ovalveolina* and *Alveolina*. A secondary tier of chamberlets may occur above this layer, *Flosculinella*, or below it, as in *Praealveolina* and *Subalveolina*. Very small, regular, upper storey secondary chamberlets are known as mansardes (attics). Alveoles are tiny chamberlets that do not run the whole length of the chamber as in *Subalveolina*. The apertures usually reflect the arrangement of the chamberlets.

All genera have a preseptal canal linking all the chamberlets of one chamber. *Alveolina* has, in addition, a postseptal canal. In *Alveolinella* the preseptal canal is doubled.

The primary chamberlets are either in line with those of preceding and subsequent chambers, *Ovalveolina*, *Praealveolina*, *Borelis* and *Alveolinella*, or they alternate as in *Alveolina*, *Bullalveolina* and *Flosculinella*.

The various genera also differ in the degree to which the early coiling is milioline.

It must be borne in mind, when attempting to apply these criteria, that both in single- and double-tiered genera the tiers of chamberlets may be multiplied towards the poles, together with addition of supplementary apertures (see figure 8.5). It should also be noted that overall shape and dimensions and whorl and chamber number, together with amount of flosculinisation, are generally considered to be of specific value only. A peculiar feature is that where the amount of flosculin varies in different whorls as it does in certain species of *Alveolina*, such as *A. globosa*, the adult size does not vary in consequence because the number of whorls appears to vary to compensate for it. This is also very marked in *A. elliptica* and must be taken into account when considering whorl number as a specific character. Polar thickening is also a valuable specific character in *Alveolina*. It tends to be confined to immature whorls, the last few, as in *A. violae,* being unthickened.

The basic morphology of *Rhapydionina* (Rhapydioninidae herein) is shown in figure 8.6.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

The existence of a cornuspirid juvenarium in the structually complex members of the Miliolida with the second chamber up to more than one turn length in some genera, together with the early appearance of the Cornuspiridae, combine to suggest that this bilocular group are the primitive rootstock from which the other families derive. The ultimate origin of the order has been considered to be from *Spirillina* (Galloway, 1933) or from *Ammodiscus* within the agglutinating group (Cushman, 1948). More recently, Arnold (1978) has shown that the Recent allogromiid, *Periptygma lunothalmia* develops a crescentic second chamber like the second chamber of the cornuspirid juvenarium and even additional arcuate, bilocular chambers. This suggests that at least some 'miliolidean' lineages might have arisen directly from an *Allogromia*-like ancestor rather than indirectly through a planispirally coiled form or through some agglutinated representative of the Saccamminidae or Ammodiscidae. This idea is given some support by the joint occurrence of both the Cornuspiridae and the earliest bilocular septate genus, *Eosigmoilina* of the Palaeomiliolinidae, in the Carboniferous. The Nubeculariidae, as here defined, do not appear until the Jurassic but the Ophthalmidiidae appear in the M. Triassic with *Eoophthalmidium.*

Wood and Barnard (1946) considered that the Ophthalmidiidae arose from *Cornuspira* but as *Eoophthalmidium* is involute it is considered more likely by Zaninetti and Brönniman (1969), followed by Copestake (1978), that the ancestor was *Hemigordius* which evolved into *Eoophthalmidium* by loss of its initial streptospiral coils and appearance of septa, producing elongate, tubular chambers. The possibility that the involute, planispiral genus *Vidalina* could be ancestral, appears to be ruled out by its late appearance in the Cretaceous. According to Wernli (1972) its presence in the Triassic and Jurassic has not been demonstrated. Similarly *Gordiospira,* cited by Hohenegger and Piller (1975) is not definitely known before the Upper Triassic.

In the Upper Triassic, *Eoophthalmidium* apparently gave rise to the evolute, flanged genera, *Ophthalmidium, Praeophthalmidium* and *Spirophthalmidium.* Species near *Ophthalmidium* also appear in the U. Trias, that show a tendency to reduce the chamber length below a half-turn length but not attaining the four-chambered whorls of *Hauerinella.* These species, referred to *'Cornuloculina'* by various authors, require further study. The appearance of annular chambers and partial partitions was apparently a late phenomenon in this family, in forms close to *Hauerinella* which gave rise to *Discospirina* in the Neogene.

The Palaeomiliolinidae appear to descend from *Eosigmoilina,* and Copestake (1978) suggests that *Palaeomiliolina* arose via the M. Trias genus *Karaburunia* and may in turn have given rise to *Edentostomina* (*Spiroloculina* of authors) as well as triloculine species such as *'Triloculina' raibliana* Gumbel near the Jurassic boundary. *Duoplanum* which Copestake considered sprang directly from *Eoophthalmidium* is without flanges and so also appears nearer to this group.

The origin of the Soritacea is unknown and the relationships between the three main families are problematical. The Soritidae appear to stem from *Peneroplis* which appeared in the Eocene and apparently show a progression through *Archaias* to the tripartite *Marginopora* in the Neogene. The Meandropsinidae which show very similar morphological trends are confined to the Upper Cretaceous and may have arisen from *Praepeneroplis.* These two groups are separated by a considerable stratigraphical gap, the 15 million year interval of the Palaeocene, during which time large soritaceans were rare or absent. The Praerhaphydioninidae are recorded from the Jurassic to the Palaeogene but again the relations between the Mesozoic and Cenozoic species must be regarded as uncertain and require further study. *Peneroplis* apparently gave rise to uncoiled cylindrical as well as discoid variants many times through the Tertiary (Colom, 1971) and the Palaeogene forms of *Haurania* and *Praerhapydionina* may have arisen by this route.

The presence of perforations in the juvenarium of *Peneroplis* has been taken as an indication of either a separate origin for the Soritidae or as indicating a perforate ancestor for the Miliolida as a whole. Thus Galloway (1933) considered that the porcelaneous group arose from *Spirillina,* while Cushman (1948) suggested that the Soritidae arose separately from the Nonionidae or even the Nummulitidae. The possibility of a perforate ancestry for the Miliolida as a whole might appear to be suggested by the apparent existence of the perforate, Triassic genus, *Miliolipora,* close

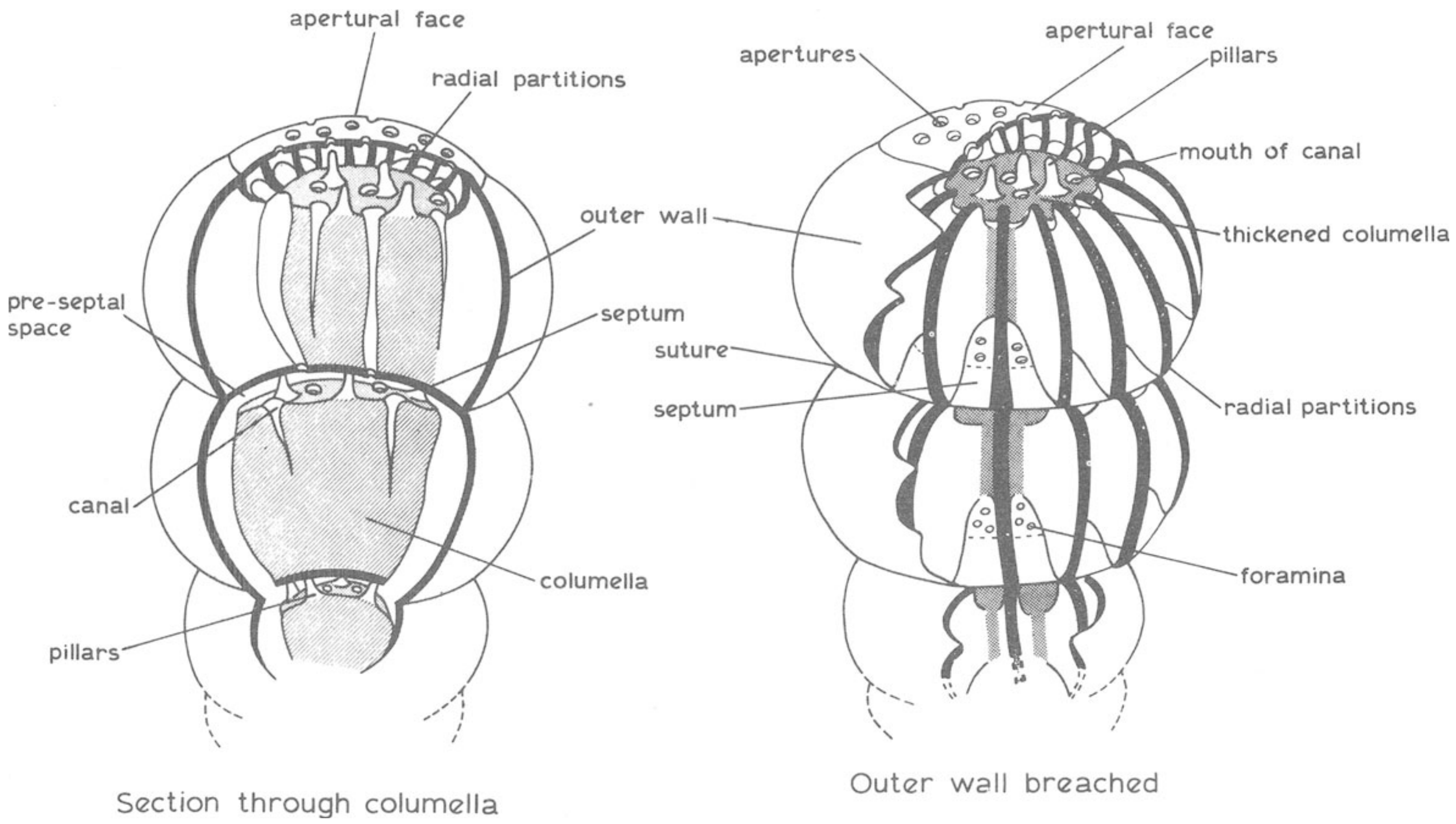


Figure 8.6 Morphology of *Rhapydionina*. After Hamaoui and Fourcade (1973), *Bull. Cent. Rech. Pau*, 7(2):361 – 435

to the Palaeomiliolinidae (Milioliporidae of Brönnimann and Zaninetti, 1971). However, none of the Soritacea show milioline juvenile or nepionic stages.

The origin of the Miliolacea is unknown. The Miliolidae apparently stem from *Quinqueloculina* which ranges (questionably) back to the Middle Jurassic. As pointed out by Copestake (1978) the source of *Quinqueloculina* is obscure but as quinqueloculine septate Miliolida are apparently absent in the Lias he suggests its origin was via *Palaeomiliolina*. On the other hand, Zaninetti and Brönnimann (1969) suggest an origin directly from the Cornuspiridae via the partially septate *Agathamminoides*. Another possibility is an origin via *Miliolipora* which is the only known Triassic, septate quinqueloculine form.

Quinqueloculina apparently gave rise to *Adelosina* in the late Jurassic but further work is required to establish whether the triloculine species which also appear then do belong to the Miliolidae and thus represent separate lines leading to *Affinetrina* and *Triloculina* s.s. The strong possibility that this was so is indicated by the appearance of both *Biloculina* and *Sinuloculina* in the Upper Cretaceous. The morphological trend towards evolute biloculine arrangement also led to the appearance of *Massilina* and *Spiroloculina* in the Cretaceous. Species of *Quinqueloculina* with outer agglutinated layer are common in the Lower Cretaceous, possibly as a response to the widespread environments favouring agglutinated Foraminifera, then widely established (see chapter 6).

Sigmoid coiling in the Miliolidae does not appear until the Tertiary and agglutinated forms along this line apparently not until the Neogene.

The relationship of the genera with miliolinellid apertural flap (Miliolinellinae) to *Quinqueloculina* is uncertain. This group appears to be restricted to the Cenozoic and is abundant in the Neogene. However, so far, fully quinqueloculine species of the genus *Scutuloris* are known only from the Recent, whereas *Biloculinella* is known from as far back as the Eocene. The quinqueloculine to triloculine *Miliolinella,* in contrast, is known to range back to the Oligocene. Despite this uncertainty, the fact that the *Miliolinella* group exhibit in full the trend from quinqueloculine to biloculine arrangement and also evolute biloculine and quinqueloculine-planispiral arrangements (see figure 8.4), lends strength to the idea that they are an independent evolutionary line worthy of subfamily or even family distinction. This group is also distinguished by the appearance of a crenulate aperture in *Crenetella* and by oblique secondary septa in *Riveroina.*

Parallel to the Miliolinellinae and showing the same range of coiling modes are genera with irregularly cribrate apertures, Cribrolinoidinae (n. subfam. herein). These are apparently restricted to the Neogene. They can be regarded as a separate line that stemmed from *Cribrolinoides* in which the aperture represents a special modification of the miliolinellid flap. However, the diversity of shapes is possibly more indicative of a polyphyletic origin for them.

The miliolids with definite round trematophore stand apart from the Cribrolinoidinae and have traditionally been divided into two subfamilies on the basis of presence or absence of partitions (see figure 8.4). This treatment probably cuts across the true lines of development. In addition, the Upper Cretaceous group, including *Idalina* (simple), *Periloculina* (incomplete partitions) and *Lacazina* (overlapping throughout), probably arose directly from the *Quinqueloculina* group, as juveniles of *Idalina* show a bar-like tooth. These genera are thus separate from the quinqueloculine *Miliola* which appeared in the Eocene. *Miliola* may have given rise to both *Fabularia* and *Lacazinella* as well as to the evolute, biloculine *Heterillina,* in the Eocene. The origin of *Austrotrillina* with its thick, alveolar wall is more uncertain and *Nevillina* may represent a separate, Neogene development. It seems clear that partitions and trematophores have arisen more than once in the Miliolidae. However, as much more research is required before the phyletic relationships of this interesting group of miliolids can be fully understood, the largely phenetic, subfamily arrangement of previous workers is still followed here.

Attempts to understand the phylogenetic relationships of the Alveolinidae are beset by similar problems. As in the case of the large soritaceans, Mesozoic genera are separated by a considerable stratigraphical break from those of the Cenozoic—in this case even longer, from the end of the Campanian to the Upper Palaeocene (see figure 8.7). The Mesozoic genera occur mainly in the early Upper Cretaceous in the Cenomanian and Turonian, and *Ovalveolina* and *Praealveolina* appear in the Albian. Apparently, only *Subalveolina* extends into the Senonian. *Cisalveolina* and *Streptalveolina* which appear to show more primitive features than *Ovalveolina* are, so far, known only from the Cenomanian – Turonian boundary. There is as yet no clear evidence of an origin within the Miliolidae as there seems to be for the Cenozoic group. These appear in the Upper Palaeocene represented by the small unflosculinised *Glomalveolina* which shows a milioline nepion in both generations (figure 8.5). *Glomalveolina* apparently gave rise to *Alveolina* near the Palaeocene – Eocene border and in this genus the milioline nepion is only found in the microspheric generation. On the face of it, this provides strong evidence of a separate origin for the Cenozoic group.

Alveolina (Fasciolites) is remarkable in that it is confined to the Eocene and appears to be the only genus of the alveolines that existed at that time. Also, as already mentioned, it is in this group that the trend to large size in the alveolines reached its fullest expression with the appearance of *A. gigantea* (up to 8.5 cm length, B form; Hottinger, 1960), and *A. levantina* (up to 10 cm length, B form; Reichel, 1964) which are among the largest Foraminifera known.

Borelis, with partial second tier of chamberlets ('Y-shaped septa'), appears to lead logically to *Flosculinella* with two tiers and *Alveolinella* with three or more. Stratigraphical support for the idea that this morphological trend is evolutionary is given by the appearance of *Borelis* as early as the Upper Eocene and *Flosculinella* and *Alveolinella* in the Neogene. As both generations in *Borelis* show a milioline nepion (Smout, 1963) and it is small and generally unflosculinised, it may have originated directly from *Glomalveolina* rather than from *Alveolina.*

The phylogenetic relations in the Rhapydioninidae have been investigated by Hamaoui and Fourcade (1973). The members of this group are held to stem from *Ovalveolina* via *Pseudedomia* in the Cenomanian which resembles *Ovalveolina* in its globular initial part but develops compressed arched chambers in its final whorls. The trend towards uncoiling is considered to have continued through the intermediate form *Murciella* to give *Rhapydionina* and *Rhipidionina* in the Senonian. Here, the stratigraphical evidence supports the suggested evolutionary relationships. Hamaoui and Fourcade also suggest that *Chubbina* and *Raadshoovenia* arose from *Ovalveolina* via an unnamed intermediate form known from the Cenomanian of Mexico. Although this seems reasonable for the Campanian *Chubbina,* it seems less likely for *Raadshoovenia* in which the type is from the Eocene and shows a markedly quinqueloculine nepion. This is more suggestive of a separate origin from within the Miliolidae.

STRATIGRAPHICAL USE OF THE MILIOLIDA

The long evolutionary history of the Miliolida from the Upper Palaeozoic to the Recent means that this order is of considerable importance in stratigraphy. The larger genera in particular are often of quite short geological range, sometimes confined to a stage, and as can be seen from figure 8.7, the ranges of some of the families, such as the Meandropsinidae, are also restricted. In the Cenozoic a number of genera do not appear until the Neogene and this includes *Discospirina,* the only known annular complex member of the Ophthalmidiidae (Adams, 1959). These groups are abundant in regions formerly part of Tethys, in countries bordering the Mediterranean, in the Middle East and in the Himalayas as well as in the Caribbean (Bignot, 1971; De Castro, 1965, 1966; Eames and Smout, 1955; Fleury, 1970, 1971; Hamaoui and Fourcade, 1973; Hamaoui and Saint-Marc, 1970; Henson, 1948, 1950a). However, at the present stage of research it is, perhaps, only the alveolines that can be applied to give a zonation which reaches the precision of the fusulinaceans discussed in the previous chapter. This applies especially to the species of *Alveolina* and *Glomalveolina* in the Palaeocene and Eocene. Figure 8.8 shows the zonal scheme drawn up by Hottinger (1960), largely on the basis of the rich assemblages of the French and Catalan Pyrenees, including the type Ilerdian of the Tremp Basin. The different *Alveolina* species groups tend to show parallel development but there is a general succession from small, primitive glomalveolines, through faunas dominated by globose and ovoid *Alveolina* species to faunas with very large cylindrical forms. Although there are differences in detail, with presence of local species, the general sequence and a number of the zones can be proved widely through the Mediterranean region including N. Italy, Sicily, Yugoslavia, Crete, Greece, Turkey and in Egypt and Libya, as shown by Hottinger and a number of other workers (Checchia-Rispoli, 1905, 1909; Doncieux, 1926; Drobne, 1975, 1977; Munier-Chalmas, 1891; Schwager, 1883b).

These alveoline faunas also penetrate into the Paris Basin (Reichel, 1937) and as far north as the Hampshire Basin in England (Adams, 1962). Only two species (*A. fusiformis* and *A.* cf. *elongata*), occur in Hampshire and in the type Bracklesham Beds (Auversian Stage) of the Isle of Wight are confined to the 10 ft (3 m) interval of Fisher Bed

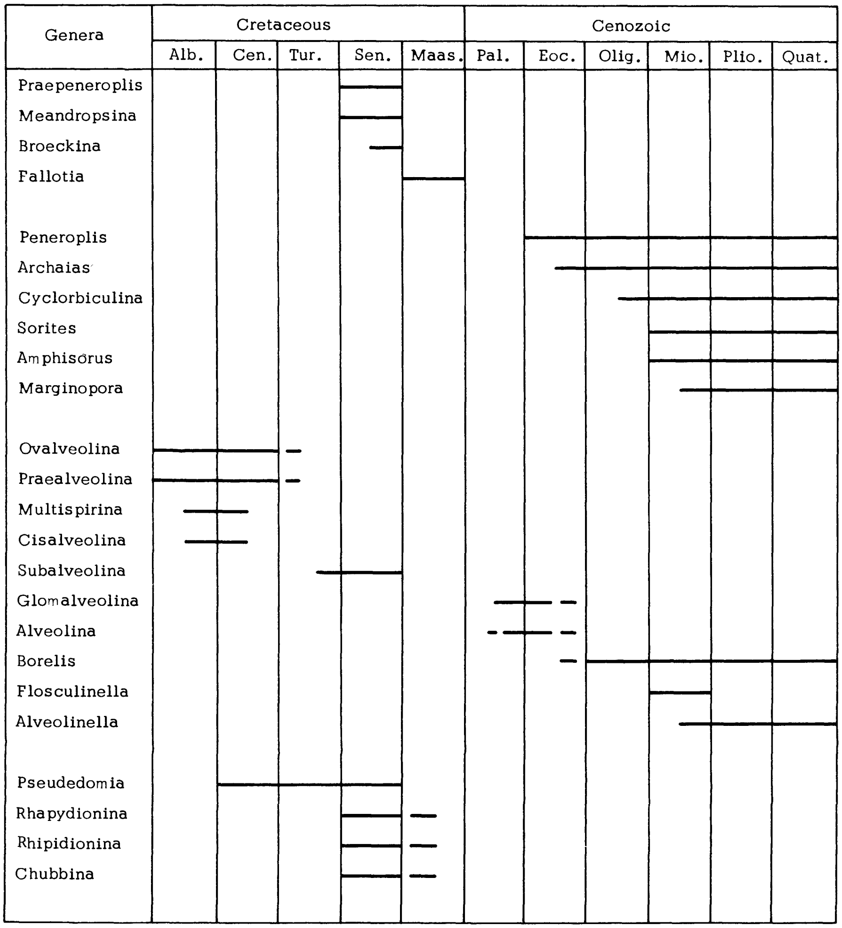


Figure 8.7 Stratigraphic ranges of Meandropsinidae, Soritidae, Alveolinidae and Rhapydioninidae. Based on various authors

XVII. This short range indicates that conditions favourable for alveolines only persisted briefly at this latitude and apparently coincided with the peak of the Eocene transgressions and consequent climatic optimum.

In general, the smaller genera of Miliolida have longer ranges and application in stratigraphy is at the species level, although the first appearance of many genera in the geological record is also of value. Perhaps their most useful application is in the early Mesozoic where the Ophthalmidiacea are a significant element in most microfaunas (Antonova, 1973; Copestake, 1978; Copestake and Johnson, 1980; Johnson, 1975; Kasimova, 1971; Zaninetti and Brönniman, 1969; Langer, 1968; Wood and Barnard, 1946; Zaninetti, 1976). Their usefulness has been enhanced by the careful evolutionary studies of *Ophthalmidium* and *Spirophthalmidium* carried out by Wood and Barnard (1946) and Copestake (1978), relating the appearance and ranges of a number of species to the ammonite zones. A similar evolutionary study has been made of *Austrotrillina,* a Tertiary member of the Miliolidae with alveolar walls, by Adams (1968). Five species are recognised and these are considered to represent a single lineage that evolved through the Oligo-Miocene. The series began with species with simple tubular alveoles (*A. striata,* range Rupelian – Aquitanian) and ended with *A. howchini,* in the late Aquitanian and Burdigalian, in which the alveoles become bifurcated and trifurcated. This lineage has useful stratigraphic application in Tethys, Asmary Limestone of Iran, and in the Indo-Pacific region.

ECOLOGY

Although extremely valuable in stratigraphical correlation the Miliolida are even more important

Biozones	Stages	Type Localities
A. elongata	Biarritzien	Biarritz
* A. prorrecta A. munieri A. stipes	Lutetian	Paris Basin
A. violae A. dainellii A. oblonga	Cuisian	Cuise la Motte
* A. trempina A. corbarica A. moussoulensis A. ellipsoidalis A. cucumiformis	Ilerdian	Tremp Basin
G. levis G. primaeva *	Thanetian	Alveolines absent in type locality London Basin

Figure 8.8 Zonal scheme for the Upper Palaeocene and Eocene based on species of *Alveolina* and *Glomalveolina*. After Hottinger (1960). *Zone distinguished by other species of Larger Foraminifera

as indicators of past environmental conditions. As mentioned above, this is because modern representatives of the order appear to be markedly restricted to certain habitats and flourish particularly in shallow water. Thus although some genera, such as *Pyrgo* and *Biloculinella,* occur at abyssal depths, possibly as part of the infauna (see chapter 4), foraminiferal faunas dominated by the porcelaneous group apparently occur exclusively in shallow water, and are characteristic of carbonate environments and hypersaline conditions (Greiner, 1969).

A high proportion of living Larger Foraminifera belong to the Miliolida, including *Sorites, Amphisorus, Marginopora, Borelis* and *Alveolinella.* Like other Larger Foraminifera these genera are restricted to warm, clear, shallow water (Cushman, 1930b; Galloway, 1933; Bandy, 1960a). They are confined to the tropics largely within the 25°C surface-water isotherms for the southern and northern summers and live down to some 33 m depth in fully marine or slightly hypersaline waters of 35 – 50 ppm (Murray, 1973b). This is because of the high temperatures required for reproduction, with possible minimum requirements of 18°C for *Sorites* and 25°C for *Amphisorus,* and because association with algal symbionts restricts them to the photic zone. As discussed in chapter 4, the relatively gigantic size of these genera is a direct result of the high levels of growth and calcium carbonate fixation achieved through this association with unicellular plants (Ross, 1974). These symbionts are known to occur both in the discoid Soritidae, which are adapted to cling both to weed as epiphytes and to sedimentary substrates, as well as in the fusiform Alveolinidae, which are epilithic on unstable open substrates. As has been explained (figure 4.7), although of very different shapes these coiling modes are of equal hydrodynamic stability. Significantly, the Soritidae apparently thin the outer wall to form transparent windows in the chamberlets (Ross, 1972c). The organic layer prevents encrustation during life but on death the windows are quickly covered.

The Soritidae are particularly abundant in seagrass, especially on genera with large, strap-shaped leaves, such as *Thalassia, Posidonia* and *Cymodocea.* Although non-encrusting and without attachment surface these annular discoid Foraminifera embed their tests in the surface mucus of the leaves. They are then able to withstand considerable current action in the surf zone and in tidal channels. Thus Davies (1970) has shown that soritids flourish in dense, subtidal meadows of *Posidonia* and *Cymodocea* down to 12 m depth in Shark Bay, Western Australia. The *Posidonia* community occurs on sandy carbonates, the *Cymodocea* community on muddy sediments. The foraminiferal associations are much the same in both, including soritids and encrusting nubeculariids as dominants, but *Marginopora* is less abundant in the *Cymodocea* community. In this area, *Alveolinella* occurs in the clean, washed, carbonate sands of the outer intertidal zone and channels. The distribution of the larger porcelaneous genera is similar in the Caribbean (Cebulski, 1969; Brasier, 1975a, 1975b, 1975c). Here *Marginopora* is absent but *Amphisorus* occurs in the *Thalasia* community in lagoonal and back-reefal environments as well as on floating weed in the surf zone. *Borelis* and *Archaias* occupy the clean, washed sands and oolites of the carbonate banks and inter-reef channels. In the Gulf of Elat, Red Sea, *Amphisorus hemprichii* and *Sorites orbiculus* occur on *Cymodocea, Halophila* and *Diplantera* down to 30 m depth, while *Borelis schlumbergeri* appears to be independent of substrate and occurs most frequently from 25 – 35 m depth (Hottinger, 1977b).

Although the smaller porcelaneous Foraminifera occupy a broader temperature and depth range than the larger genera, they also reach maximum diversity and dominate the microfaunas in tropical carbonate environments. This is well shown by recent studies in the Persian Gulf (Murray, 1965, 1966a, 1966b, 1970a, 1970b; Evans *et al.,* 1973; Seibold *et al.,* 1973; Hughes Clarke and Keij, 1973) and in the Caribbean (Bock and Moore, 1968; Brasier, 1975a, 1975b, 1975c; Wright and Hay, 1971). These faunas occupy both normal marine and hypersaline environments with salinities up to 70 ppm. A good example is the fauna of the Abu Dhabi Lagoon (Murray, 1965, 1970a, 1970b) on the south-east side of the almost land-locked Persian Gulf. Salinities range from 42 to 70 ppm and the Foraminifera live mainly in seaweed and seagrass (*Halodule*). The most abundant genera are *Peneroplis, Quinqueloculina* and *Triloculina.* These Foraminifera apparently graze on the unicellular algae and bacteria on the weed. Few Foraminifera are found in the sediment because it is too actively moved and clean to provide food. The marked dominance of the Miliolida in the coastal areas of the Persian Gulf is also well brought out by figure 8.9, which is based on the work of Hughes Clarke and Keij (1973).

The importance of seagrass, especially *Thalassia,* in providing both a habitat and a means of dispersal for epiphytic Foraminifera has been demonstrated by the work of Bock (1969) and Brasier (1975b) in the Caribbean. It is clearly a major factor in the success of the smaller as well as the larger porcelaneous Foraminifera in shallow water carbonate environments. Apart from peneroplids, the most abundant genera are members of the Miliolidae. This has prompted Arnold (1964) to suggest that the characteristic tooth structure in this family functions as a clip, enabling genera such as *Spiroloculina* to fasten on filamentous weed.

It was pointed out previously (chapter 4) that the elongate to ovate shape of many miliolids is adapted both to a vagrant life in weed and to an infaunal life in the sediment. Brasier (1975c) has attempted a general correlation of morphology with habitat in Caribbean carbonate environments. He finds that ovate, thin-shelled unornamented miliolids without a well-developed neck predominate among the epiphytic Foraminifera. *Miliolinella* with its restricted aperture is prominent in this group. On and within stable, generally vegetated, sedimentary substrates, species of *Quinqueloculina, Triloculina* and *Adelosina* with narrow tests predominate. These are often ornamented and possess produced necks. The test wall is thin in fine sediments and thick in coarse sediments with less than 40 per cent fines. On unstable sedimentary substrates, such as shore sands and sand blankets, thick-walled forms are again characteristic, usually ornamented and with large rectangular apertures. Agglutinated species are common in this environment also.

Similar faunas occur in the Mediterranean (Blanc-Vernet, 1969; Lecalvez & Lecalvez, 1958; Perath, 1966) and although soritids and peneroplids are absent, faunas with a high proportion of miliolids also occur in temperate waters. These cool water microfaunas occur in the weed zone of the littoral and immediate sublittoral, where *Massilina* and *Miliolinella* are prominent, and have been studied particularly along the Welsh Coast (Atkinson, 1969, 1971; James, 1965; Thomas, 1973). They also occur in areas of shelly carbonate sand accumulation, mainly below 29 – 30 m with *Quinqueloculina* ex gr. *seminulum* as a dominant, in the English Channel (Dupeuble, 1963; Dupeuble *et al.,* 1971; Murray, 1970c) and the St. Georges Channel area (Dobson *et al.,* 1971; Haynes, 1973; James, 1973; Parrish, 1972). The role of laminarian holdfasts in providing shelter for genera such as *Massilina* and *Quinqueloculina* in the wave zone and the influence of weed types on the populations of epiphytes has also been studied by James (1965) and Thomas (1973).

The occurrence of large porcelaneous genera within narrow geographical limits at the present day means that sediments containing fossil representatives of this group can be interpreted as deposited in warm, shallow water with reasonable confidence and precision. Thus all occurrences of fossil alveolines are regarded as neritic (Inner Shelf) by Reichel (1964), restricted littoral and tropical (Dilley, 1973) and protected shelf and reef shoal (Hottinger, 1973). Further, the presence of *Borelis curdica* in the Miocene of the Isle of Cos, Greece, is held to indicate very shallow clear water of the order of 1 m in depth, temperatures from 25 – 30°C, strong currents and salinities ranging from normal marine, 35 ppm, to slightly hypersaline, 50 ppm (Bignot and Guernet, 1976). Limestones of Miocene Age with this species occur widely through Turkey and the Middle East, and in Libya (subsurface, Sirtica) it is found associated with abundant fruiting bodies of dasycladacian algae in a matrix of sparry calcite, again indicative of very shallow water. Similarly, the large genera of the Rhapydioninidae, such as *Pseudedomia,* are considered to represent warm, shallow water of normal marine salinity (Hamaoui and

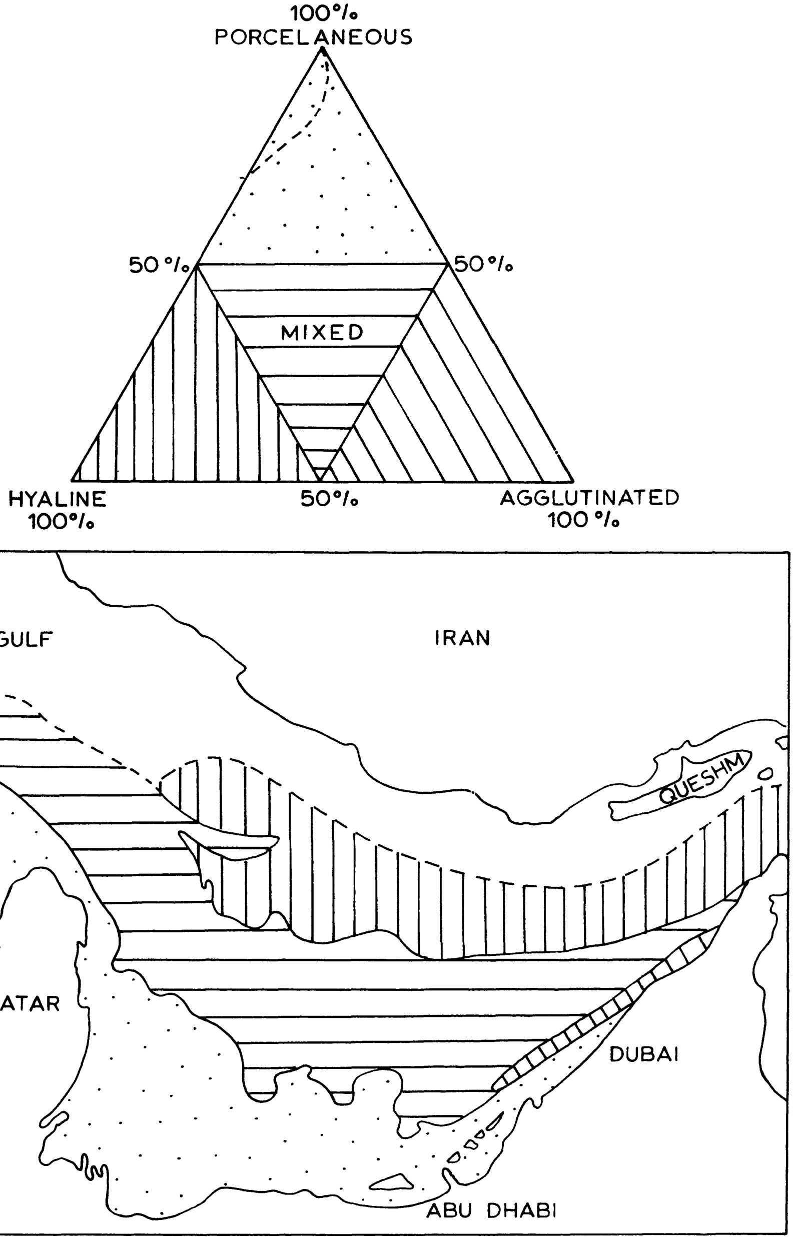


Figure 8.9 Distribution of the major wall structure groups in the Persian Gulf (where >50 per cent, as shown on the triangular diagram after plotting of foram samples according to percentage). The shallower southern part of the gulf is dominated by the porcelaneous group, intermediate depths by a mixed assemblage and the deeper parts by hyaline forms. Samples from Abu Dhabi (Murray, 1970a, 1970b) and Barbuda (Brasier, 1975b) fall within the very restricted field shown by the dotted line on the triangle, almost 100 per cent porcelaneous. After Hughes Clarke and Keij (1973)

Fourcade, 1973). The association of *Rhapydionina* with abundant charophyte oogonia in certain Balkan localities led these authors to suggest this genus could withstand waters of lowered salinity (brackish). However, the possibility must be considered that these algal fruiting bodies were derived from nearby land, as in the case of abundant charophyte oogonia in the fully marine Quaternary on the shelf off S.W. Africa (Mcmillan, pers. comm.).

The distribution of these large miliolaceans is consistent with the former position of the tropical belt and they reached great abundance along the borders of the east and west, Tethyan seaway. The distribution of the large, annular-discoid soritaceans is very similar and as they are commonly associated with seagrass today, extinct members of the group such as *Orbitolites* and the Meandropsinidae are presumed to have had the same habit (Wright and Murray, 1972; Brasier, 1973, 1975d). These genera have thus been used to indicate the former presence of submarine grasses back to the Cretaceous, and Brasier (1975d) has attempted to distinguish separate *Zostera* (including *Posidonia*), *Cymodocea* and *Thalassia* (including *Halodule*) communities. However, care must be taken not to push this idea too far. The fossil evidence for the existence of fully marine grasses in the Cretaceous is poor, although good for the Palaeogene of the Hampshire and Paris Basins (Curry, 1965; Den Hartog, 1970). Further, soritids are not confined to seagrasses and *Amphisorus* has been described as thriving equally well both on fibrous and on non-fibrous weed as well as on soft sediment (Brasier, 1975a). Again, as noted in chapter 3, *Marginopora* has been described by Ross (1972c) as epilithic on reefal, carbonate sands which it is able to bind into a loose aggregate, capable of withstanding considerable current action. The student should also note that *Peneroplis planatus* and *Marginopora vertebralis* occur on both *Posidonia* and *Cymodocea* in Shark Bay (Davies, 1970). In Abu Dhabi lagoon *Peneroplis planulatus* occurs on *Halodule,* as the most abundant foraminifer, together with *Peneroplis pertusus* (Murray, 1970a, 1970b). In Barbuda, West Indies, *Peneroplis pertusus* and other peneroplids are described as preferring fibrous weed (Brasier, 1975c). In the Gulf of Elat, although *Sorites orbiculus* is epiphytic, *Sorites orbitolitoides* also occurs on hard substrates such as dead coral, molluscs and pebbles, often as an encrusting form (Hottinger, 1977b). This strongly suggests that the seaweeds and seagrasses provide general shelter and that the various porcelaneous genera and species are not restricted to a particular host ('host specific'). The strong link between the Soritidae and seagrass appears to be simply a result of the favourable surface of attachment provided by the mucous coating of the strap-shaped leaves. Work off the coast of Wales (Atkinson, 1969, 1971; Haynes and Dobson, 1969; Haynes, 1964; Dobson and Haynes, 1973; James, 1965; Thomas, 1973) also confirms the generalised role of the weed, including hydroids, in providing shelter for epibiotic Foraminifera, including members of the Miliolidae.

Small miliolids commonly occur as constituents of alveoline limestones and are commonly the major element in shallow water limestones from the Upper Cretaceous onwards, as in the Middle Eocene Calcaire Grossier of the Paris Basin (Wright and Murray, 1972).

The interpretation of sediments with a high proportion of ophthalmidiids is more speculative as they are rare at the present day, but most authors assume their environmental preferences were similar to those of the miliolids. Thus Gordon (1970), in his work on Jurassic environments, considered microfaunas with *Ophthalmidium* making up more than a quarter of all specimens to be shallow water. This general line of reasoning was followed by Brooke and Braun (1972) in their interpretation of the Upper Jurassic, Shaunavon, of Saskatchewan. Similarly, Copestake (1978) found that peak abundance of *Ophthalmidium* in the Lower Lias of Mochras (Wales) coincided with maximum diversity of Ophthalmidiacea and Nubeculariacea as a whole and interpreted these assemblages as shallow water. The occurrence of algal-coated specimens of *Ophthalmidium* as a limestone former in the Lower Lias of Poland (Gazdzicki, 1975) seems to provide strong support for this idea.

The flattened, blade-like form of the ophthalmidiids with extended apertures may have been an adaptation to feeding at the sediment – water interface with the capability of orientation to the currents. The ovate-elongate palaeomiliolinids probably lived in the sediment like the morphologically similar miliolids but the strong trend to flattened bilocular form in some genera of the group may, as in the parallel case of *Massilina* and *Spiroloculina,* indicate adaptation to a phytal habitat.

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SUMMARY CLASSIFICATION

MAIN FAMILIES AND IMPORTANT GENERA OF MILIOLIDA

MILIOLIDA	wall porcelaneous, or secondarily agglutinated; normally with bilocular juvenarium; second chamber narrowed to a flexostyle in advanced forms; U. Palaeoz. – Rec. Key figures 8.10 to 8.13.
NUBECULARIACEA n. superfam.	bilocular, or with bilocular juvenarium followed by irregular chambers, planispiral or in various planes, to uncoiled and irregular, aperture simple, round or slit; Carb. – Rec. Key figure 8.10.
CORNUSPIRIDAE *nom. transl.* (= Cornuspirinae)	proloculus followed by undivided tubular or spreading second chamber; Carb. – Rec.
Gordiospira (no. 1)	tube in juvenile wound in various planes, adult planispiral and partially involute; ? Carb. – Rec. (involute = *Hemigordius* (nos. 2/3), Carb. – Jur.; globular = *Hemigordiopsis,* Perm.; zig-zag coil = *Meandrospira,* Carb. – Lias.).
Cornuspira (nos. 4/5)	conserved name (Melville 1978) tube evolute planispiral; Carb. – Rec. (tube in adult flattened and spreading = *Cornuspirinoides,* Rec.; spreading and branched = *Cornuspirella,* Rec.; involute = *Vidalina,* U. Cret.).
Agathammina (nos. 6/7)	tube coiled in various planes to give irregularly quinqueloculine test; Carb. – ?Jur. (incipient septation = *Agathamminoides* Zaninetti 1969, Trias).
Calcitornella (no. 8)	attached, tube planispiral to uncoiled and irregular with transverse thickenings resembling septa; Carb. – Perm. (juvenarium followed by uncoiled, zig-zag tube = *Calcivertella*).
NUBECULARIIDAE	bilocular (cornuspirid) juvenarium followed by irregularly sized chambers, planispiral with 3 or more per whorl, or irregularly uncoiled and uniserial; Jur. – Rec.
Fischerina (nos. 9/10)	evolute planispiral with high arched aperture; ?Cen. (involute with numerous chambers = *Nautiloculina,* Jur.; involute and compressed with slit-like aperture = *Planispirinella,* Cen.).
Nubecularia (nos. 13/14)	attached, adult irregularly uncoiled and may grow away from substrate as tube, aperture a basal slit when attached, round with infolded rim when growing away; Jur. – Rec. (adult uniserial and more regularly chambered = *Nubeculinella,* U. Jur.; chambers with stolon-like necks = *Nubeculina,* Rec.).
Calcituba (no. 11)	attached, uniserial with irregularly elongate chambers; Rec. (few chambers and fimbriate keel = *Webbina,* Rec.).
Nodobacularia (no. 12)	attached, single coil of 2 – 3 chambers followed by uniserial, pyriform chambers; Lias. (free, adult uniserial with elongate, compressed chambers = *Nodophthalmidium,* Rec.).
OPHTHALMIDIACEA n. superfam.	bilocular juvenarium followed by elongate, tubular chambers, planispiral or in various planes, aperture simple; Carb. – Rec. Key figure 8.10.

PALAEOMILIOLINIDAE n. fam.	chambers two per whorl in various planes; Carb. – Rec.
Eosigmoilina (no. 15)	second chamber of juvenarium irregularly coiled, adult chambers evolute sigmoid; Carb. – ?M. Trias. (adult involute sigmoid = *Karaburunia* Langer 1968, M. and U. Trias).
Palaeomiliolina (nos. 16/17)	irregularly quinqueloculine to evolute biloculine; U. Trias. – Jur.
Edentostomina (nos. 18/19)	evolute biloculine; U. Trias. – Rec. (agglut. = *Psamminopelta*, Lias. – U. Cret.; adult chambers in 2 (sometimes 3) planes at right angles = *Duoplanum* Copestake in Copestake and Johnson 1981, U. Trias. – Lias.).
OPHTHALMIDIIDAE	planispiral with chambers becoming reduced from more than one whorl length to regularly bilocular, in evolute forms separated by a plate-like flange. Advanced forms show reduction to 3 or 4 chambers per whorl and also annular growth with partial subdivision; M. Trias. – Rec.
Eoophthalmidium Langer 1968 (nos. 20/21)	involute without flange, second chamber of juvenarium over 2 whorls length, adult chambers about ¾ turn; M. Trias. – ?L. Jur.
Praeophthalmidium Knauff 1966 (no. 24)	evolute, with flange, second chamber of juvenarium up to 4 whorls, but generally 2, adult chambers 1 per whorl; U. Trias. – M. Jur.
Ophthalmidium emend. Copestake in Copestake & Johnson 1981 (nos. 22/23)	evolute, with flange, second chamber of juvenarium up to 1¼ turns, first adult chamber variable and may be up to 1½ turns (A form), later chambers generally ¾ turn with the last one or two of ½ turn length; U. Trias. – Rec.
Spirophthalmidium (no. 27)	evolute, with flange, second chamber of juvenarium up to 2 turns, adult chambers of ½ length, abruptly succeed juvenarium regularly at 2 per whorl (A form); ?U. Trias. – Rec.
Hauerinella (nos. 25/26) = *Cornuloculina nom. oblit.*	evolute, with flange, second chamber of juvenarium up to 3 turns (A form), first adult chamber up to 1½ turns, later chambers generally ¾ turn reducing to ⅓ and ¼ turn in final whorls; ?Jur. – Rec. (final chambers flabelliform to annular with partial partitions extending towards roof, aperture a single row of pores and slits at periphery = *Discospirina*, Neo. – Rec.).

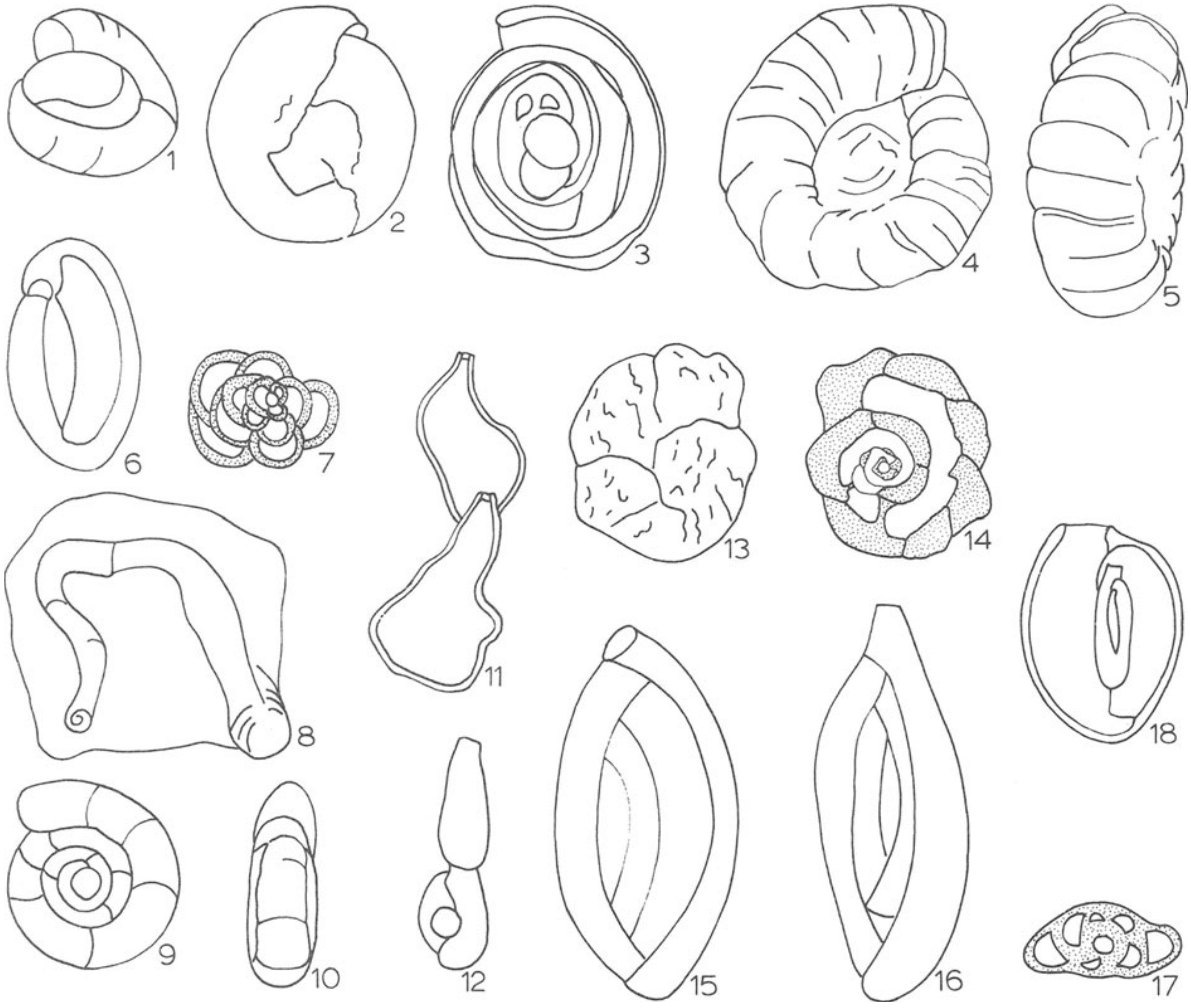
N.B. *Ophthalmidium inconstans* (Brady) was designated as holotype of *Hauerinella* Schubert (1921) by Wood and Barnard (1946). The authors also provided a clear description of both the microspheric and megalospheric generations. Despite this, the name *Cornuloculina* Burbach (1886) was revived by Loeblich and Tappan (1964), again with designation of Brady's species as holotype. As proper validation of *Hauerinella* clearly antedates that of *Cornuloculina* the spirit of the Rules of Nomenclature would seem to be best served by considering Burbach's name a forgotten name under the fifty-year rule, as proposed by Langer (1968).

SORITACEA n. superfam.	planispiral to uniserial, flabelliform or annular, generally developing incomplete partitions or chamberlets, aperture multiple; Jur. – Rec. Key figure 8.11.
SORITIDAE	involute planispiral to uncoiled or evolute, annular discoid with partial or complete partitions, several tiers of chamberlets in advanced forms; Eoc. – Rec.
Peneroplis (nos. 3/4)	planispiral lenticular, becoming uncoiled and flaring or cylindrical, apertures multiple row in the median line; Eoc. – Rec. (aperture dendritic = *Dendritina;* aperture terminal = *Spirolina;* cribrate = *Cribrospirolina* Haman 1972, 1976).
Archaias (nos. 5 – 7)	planispiral involute to evolute annular with irregular interseptal pillars, apertures multiple row on periphery; M. Eoc. – Rec. (regular partitions = *Cyclorbiculina,* U. Olig. – Rec; fusiform = *Fusarchaias,* Olig. – Mio. median partition through chamberlets = *Androsina,* Rec. Lévy, 1977).
Sorites (nos. 14/15)	peneropline nepion, adult annular discoid with low chamberlets connected to each other and to those in adjacent chambers by stolons; apertures 2 per chamber at periphery; Mio. – Rec. (without stolons between adjacent chambers, annulae numerous and poorly defined in later stages with thick walls = *Orbitolites,* U. Pal. – Eoc.).
Amphisorus (nos. 12/13)	nepion reduced to one chamber; adult a biconcave disc with 2 partial layers of chamberlets; apertures in 2 alternating rows in depressions on the periphery; Mio. – Rec.
Marginopora (no. 16)	nepion a single equatorial chamber; adult a large, biconcave disc, initially with 2 layers of annular chambers divided into chamberlets, later with an expanding wedge of low chambers inserted between them, incompletely subdivided into vertically elongate, equatorial chamberlets; undivided reproduction chambers may be added finally (usually broken off); lateral chamberlets alternate with the rows of equatorial chamberlets and communicate by stolons above and below; apertures multiple in vertical rows on the periphery; Mio. – Rec.
MEANDROPSINIDAE	planispiral to annular discoid, usually involute and with partially developed partitions; Upper Cret.
Praepeneroplis (nos. 1/2)	close-coiled with triangular chambers; Sen. (becoming evolute annular, without pillars or partitions = *Vandenbroeckia;* incomplete partitions = *Broeckina,* Camp.; involute planispiral throughout with partial partitions = *Fallotia,* Maas., with incomplete partitions and involute but compressed and becoming annular = *Meandropsina,* Sen.).
PRAERHAPYDIONINIDAE (*nom. transl.* Hamaoui and Fourcade, 1973)	planispiral involute to uniserial conical or flabelliform with incomplete radial partitions and interseptal pillars; Jur. – Olig.
Haurania (nos. 8 – 10)	planispiral involute to uniserial conical with incomplete vertical partitions, aperture cribrate; Jur. – Eoc. (aperture terminal and single =

	Praerhapydionina, U. Cret. – Olig.).
Pseudorhipidionina De Castro, 1971 (no. 11)	adult chambers compressed, low and arched (flabelliform); Jur. – Eoc.
MILIOLACEA	chambers winding, planispiral fusiform with spiral septula, or uncoiled cylindrical or compressed with partial partitions and thickened central zone; aperture dentate, with trematophore, or cribrate; Jur. – Rec. Key figures 8.12 and 8.13.
MILIOLIDAE	chambers winding in various planes about a longitudinal axis, generally 2 per whorl, aperture dentate, cribrate or with trematophore and alternating from end to end; chambers simple or with vertical partitions; Jur. – Rec. Key figure 8.12.
Quinqueloculina = *Lachlanella* (nos. 3/4 and figures 8.2 and 8.3)	chambers added successively at about 140 – 150° to each other, giving a quinqueloculine to quadriloculine test with 4 (or 3) chambers visible in front view, 3 in rear view; aperture flush and oval to rectangular, tooth bar-like with minutely bifid end; ?M. Jur. – Rec. (aperture produced and round with short, bifid tooth = *Adelosina* = *Cycloforina* Luczkowska 1972 (nos. 1/2); wall fully agglutinated = *Miliammina,* Cret. – Rec.; supplementary teeth = *Podolia,* Mio.; ring-like toothplate = *Cribrolinoides,* Plio. – Rec.; adult loosely planispiral = *Ptychomiliola,* Rec.).
Affinetrina Luczkowska 1972 (nos. 5/6)	chambers added successively at about 140 – 120° to each other, giving a quinqueloculine to triloculine test with 3 chambers visible in front view, 2 in rear view; aperture flush and oval to rectangular, tooth bar-like with minutely bifid end; ?Neogene – Rec. (aperture round with short bifid tooth = *Triloculina* (no. 7), ?Jur. – Rec.; aperture a cruciform slit = *Cruciloculina* (no. 8), Plio. – Rec.).
Biloculina (nos. 9/10)	chambers added successively at 140 – 180° to each other, giving a quinqueloculine to involute, biloculine test, 2 chambers visible in front view as final chamber clasps penultimate all round; aperture oval with bar-like tooth; U. Cret. – Rec. (aperture round with short, bifid or wedge-shaped tooth = *Sinuloculina* (nos. 13/14), U. Cret. – Rec.).
Massilina (figures 8.2 and 8.3)	chambers added successively at 140 – 180° to each other, giving a quinqueloculine to evolute, biloculine test; aperture oval to rectangular with bar-like tooth; Cret. – Rec. (A forms completely biloculine by end of first set of chambers (5) or throughout = *Spiroloculina;* irregularly cribrate = *Tortonella,* Mio.).
Sigmoilina (nos. 11/12)	chambers added successively at 120 – 180° to each other in a sigmoid spiral to give a laminated, involute test; aperture round with short bifid tooth; Eoc. – Rec. (less involute and with outer agglutinated layer = *Sigmoilopsis,* Neo. – Rec.; final whorls evolute biloculine = *Spirosigmoilina,* Mio.).
Miliolinella (nos. 17/18)	chambers added successively at about 140 – 150° to each other which, together with twisting of the axes, gives a flattened quinqueloculine to triloculine test;

	aperture semicircular with broad flap-like toothplate, almost filling the opening (often broken out); ?Olig. – Rec. (regularly quinqueloculine = *Scutuloris,* Rec.; tooth reduced and quadrangular = *Varidentella* Luczkowska 1972, Neo. – Rec.; early stage planispiral = *Planispirinoides,* Rec.; crenulate aperture = *Crenetella* (nos. 23/24), Mio.).
Pyrgo (nos. 15/16)	chambers added successively at about 140 – 180° to give a quinqueloculine to involute biloculine test, 2 chambers visible in front view, the final chamber clasping the penultimate all round; aperture semicircular or compressed with reduced, subquandrangular toothplate which may have hooked or rounded ends; ?Neo. – Rec. (toothplate a broad high flap that tends to fill the aperture = *Biloculinella,* Eoc. – Rec.; aperture of chevron-shaped slits = *Pyrgoella,* Quat.; irregularly cribrate = *Cribropyrgo,* Rec.)
Flintia (nos. 19/20)	chambers added successively at 180° to give an evolute, biloculine test, aperture semicircular with reduced subquadrangular flap; Rec. (oblique secondary septa = *Riveroina,* Rec.).
Nummoloculina (nos. 21/22)	chambers milioline (subquinqueloculine) to involute planispiral with up to 6 chambers in each whorl, aperture semicircular with broad flap-like tooth; Neo. – Rec. (globular and irregularly cribrate = *Involvohauerina*, Rec.).
Miliola (nos. 25/26)	chambers added successively at about 140 – 150° to each other to give a quinqueloculine test; aperture round with trematophore; Eoc. (quinqueloculine to evolute biloculine, = *Nevillina,* Rec.; chambers in more than 5 planes = *Schlumbergerina,* Rec.).
Idalina (nos. 27/28)	chambers added successively at 140 – 180° to each other to give a quinqueloculine to biloculine test, the final chambers overlapping to give an, apparently, single-chambered adult, aperture with regularly perforated trematophore in final stage; U. Cret.
Heterillina (no. 29)	chambers added successively at 140 – 180° to each other to give a quinqueloculine to evolute biloculine test, aperture round with irregularly perforated trematophore; Palaeogene (agglutinated exterior = *Ammomassilina,* Rec.; planispiral in adult stage with 3 or more chambers to the whorl = *Hauerina,* Eoc. – Rec.; more than 3 chambers and with partitions = *Pseudohauerina* Ponder 1972).
Fabularia (no. 30)	chambers added successively at 140 – 180° to each other to give a quinqueloculine/quadriloculine to involute biloculine test, subdivided by thick vertical partitions into elongated chamberlets with 2 tiers in outer whorls; aperture with irregularly perforated trematophore; M. Eoc. – Rec. (triloculine with thick alveolar wall = *Austrotrillina,* Olig. – Mio.; adult chambers completely overlapping, vertical partitions incomplete = *Periloculina,* U. Cret.; completely overlapping chambers throughout = *Lacazinella,* U.Eoc.; depressed discoid = *Lacazina,* U. Cret.).

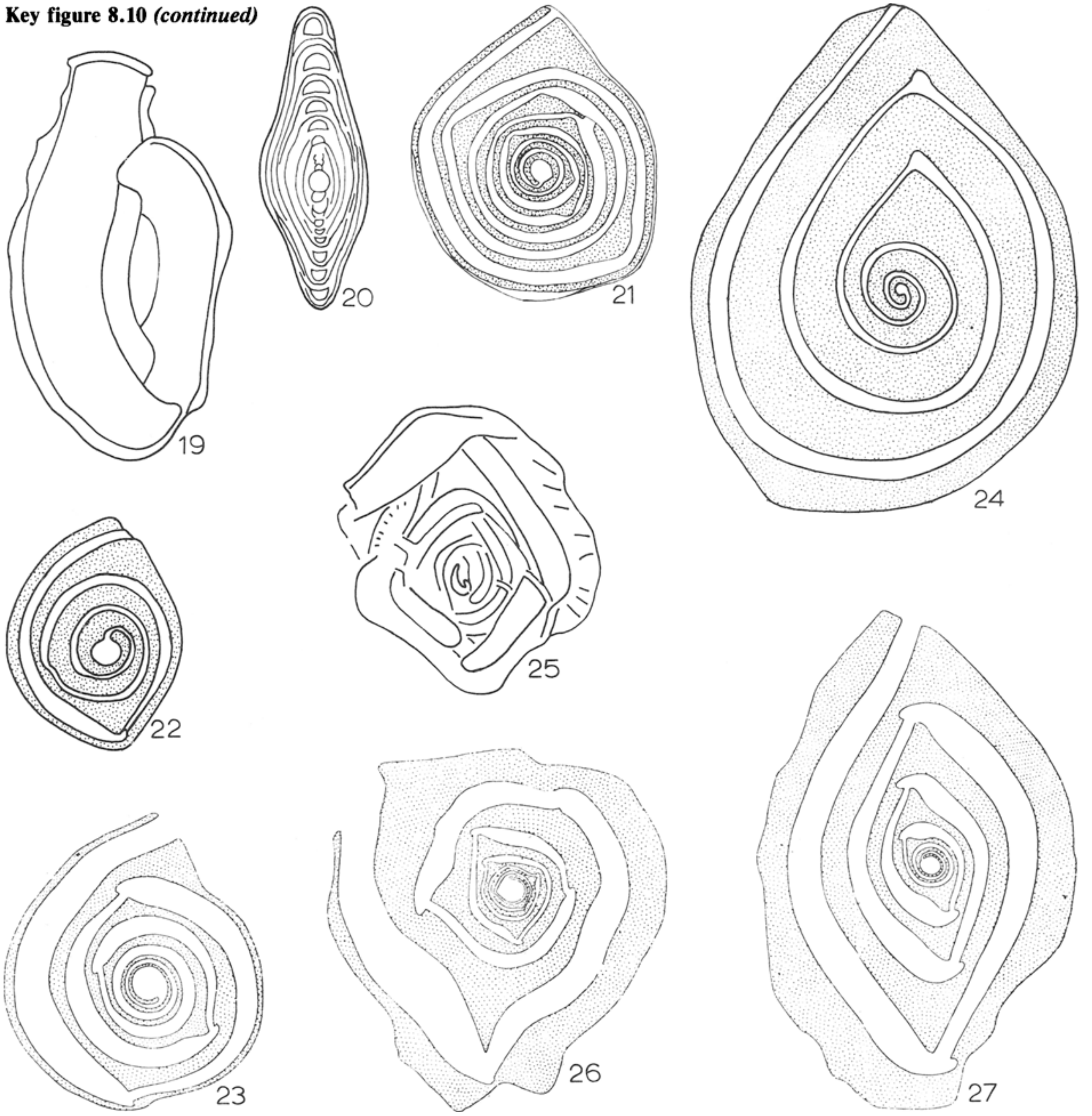
ALVEOLINIDAE	test large, planispiral-fusiform, cylindrical or globular, early whorls may be irregular or milioline; chambers divided into chamberlets by spiral septula, horizontal partitions may produce several tiers; chamberlets connected along the chamber by passages; apertures numerous; L. Cret. – Rec. Key figure 8.13.
Ovalveolina (no. 2)	ovoid, single tier of chamberlets with wide spaced septula, 1 row of apertures, pre-septal passage only; Alb. – Tur. (wide post-septal passage and long, low aperture = *Cisalveolina,* Cen. – Tur.; streptospiral = *Streptalveolina* Fourcade *et al.* 1974, Cen.).
Praealveolina (no. 1)	single tier of chamberlets and 1 row of apertures at equator, but small secondary chamberlets appear below them laterally and there may be several tiers, with numerous apertures, at the poles; pre-septal passage only; Alb. – Tur. (single tier of chamberlets only = subgenus *Simplalveolina,* Cen.; double row of apertures with upper foramina connecting with alveoli = *Subalveolina,* Camp.; intercalated whorls and sutural apertures = *Multispirina,* Cen.).
Alveolina = *Fasciolites* (no. 4)	single tier chamberlets, although may be doubled with attics appearing towards poles; pre-septal and post-septal passages; 2 rows of apertures, the upper connecting with the pre-septal passage; floor of chamber thickened and may be heavily flosculinised; U. Pal. – Eoc. (small, spherical with unthickened floor = subgenus *Glomalveolina* (no. 3), M. Pal. – Eoc.; bilocular = *Pseudofabularia* Robinson 1974, M.Eoc.). N.B. There are strong arguments for the conservation of the name *Alveolina,* see Smout, 1963.
Borelis (no. 5)	small, partial second tier alternating with primary chamberlets, giving 'Y-shaped' septa; pre-septal passage only; U. Eoc. – Rec. (several rows of apertures, the upper opening into alveoli = *Bullalveolina* (no. 6), Olig.).
Flosculinella (no. 7)	secondary tier of attics above primary chamberlets, 2 rows of apertures; floor thickened in axial zone, pre-septal passage only; Mio.
Alveolinella (no. 8)	elongate fusiform, several tiers of chamberlets and numerous apertures; pre-septal passage doubled; Mio. – Rec.
RHAPYDIONINIDAE *nom. transl.* (= Rhapydioninline)	planispiral or streptospiral to uncoiled compressed, flabelliform or cylindrical; early whorls may be milioline; with partial vertical partitions, central zone with canaliculate thickening except for a pre-septal space with buttresses (residual pillars); U. Cret.
Rhapydionina (figure 8.6)	planispiral to uncoiled cylindrical; Sen. – ?Maas. (test compressed with low arched chambers (flabelliform) = *Rhipidionina;* involute lenticular with compressed flange of low arched chambers = *Pseudedomia* emend. Smout, 1963), Cen. – Sen.; globular and streptospiral to planispiral = *Chubbina* Robinson 1968, Camp.).



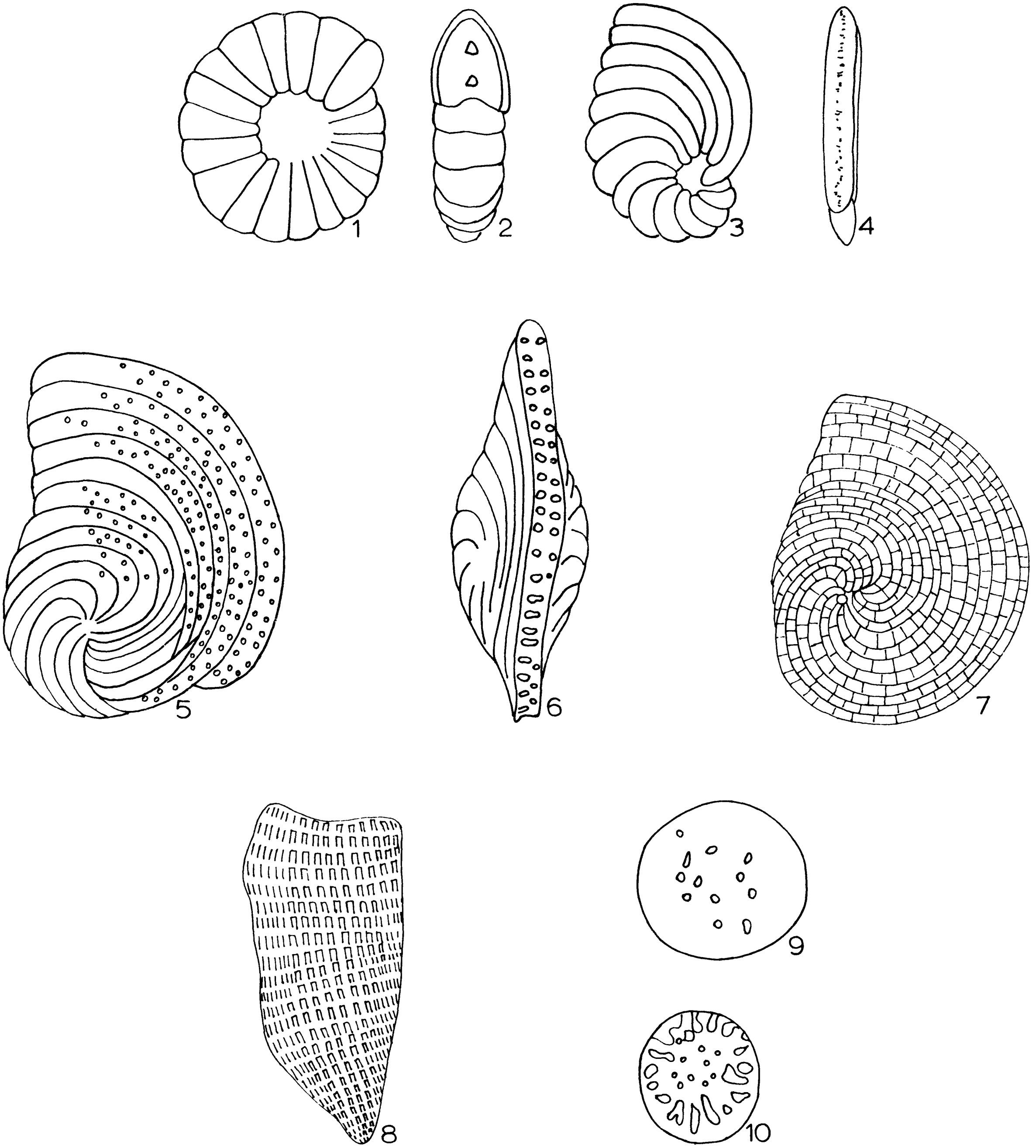
Key figure 8.10 Nubeculariacea, Ophthalmidiacea, Cornuspiridae, Fischerinidae, Palaeomiliolinidae, Ophthalmidiidae

1 ***Gordiospira fragilis*** **Heron-Allen & Earland, paratype after L. & T., × 102**
2/3 ***Hemigordius schlumbergeri*** **(Howchin), 2 side view, 3 section, approx. × 42**
4/5 ***Cornuspira selseyensis*** **Heron-Allen & Earland, from Haynes, 4 side view, 5 apertural view, × 70**
6/7 ***Agathammina pusilla*** **(Geinitz), after Vašíček & Růšička, 6 side view, 7 horizontal section, × 161**
8 ***Calcitornella grahamensis*** **(Harlton), holotype, after L. & T., × 25**
9/10 ***Fischerina rhodiensis*** **Terquem, 9 side view, after Terquem, 10 apertural view, after L. & T., × 53**
11 ***Calcituba polymorpha*** **(von Roboz), optical section, after L. & T., × 105**
12 ***Nodobacularia tibia*** **(Jones & Parker), lectotype, after L. & T., × 70**
13/14 ***Nubecularia ex gr. lucifaga*** **Defrance, 13 dorsal view, 14 attachment surface, after Brady, × 102**
15 ***Eosigmoilina explicata*** **Ganelina, front view, × 140**
16/17 ***Palaeomiliolina occulta*** **Antonova, 16 front view ?, 17 horizontal section, × 224**
18 ***Edentostomina milletti*** **(Cushman), vertical section, after Millett, × 28**

Key figure 8.10 ***(continued)***



19 ***Edentostomina cultrata*** **(Brady), front view, after Millett, × 28**
20/21 ***Eoophthalmidium tricki*** **Langer, 20 axial section, 21 vertical section, × 70**
22 ***Ophthalmidium liasicum*** **(Kübler & Zwingli), vertical section, after Copestake, A form, × 280**
23 ***Ophthalmidium margaritifera*** **(Heron-Allen & Earland), vertical section, from Wood & Barnard, × 140**
24 ***Praeophthalmidium orbiculare*** **(Burbach), vertical section, diagonal, after Knauff**
25/26 ***Hauerinella inconstans*** **(Brady), 25 side view of holotype, × 21, 26 vertical section, topotype, after Wood & Barnard, × 35**
27 ***Spirophthalmidium acutimargo*** **(Brady), vertical section, after Wood & Barnard, × 105**



Key figure 8.11 **Soritacea, Soritidae, Meandropsinidae, Praerhapydioninidae**

1/2 ***Praepeneroplis senoniensis*** **Hofker, after Loeblich & Tappan, 1 side view, 2 apertural view, × 60**

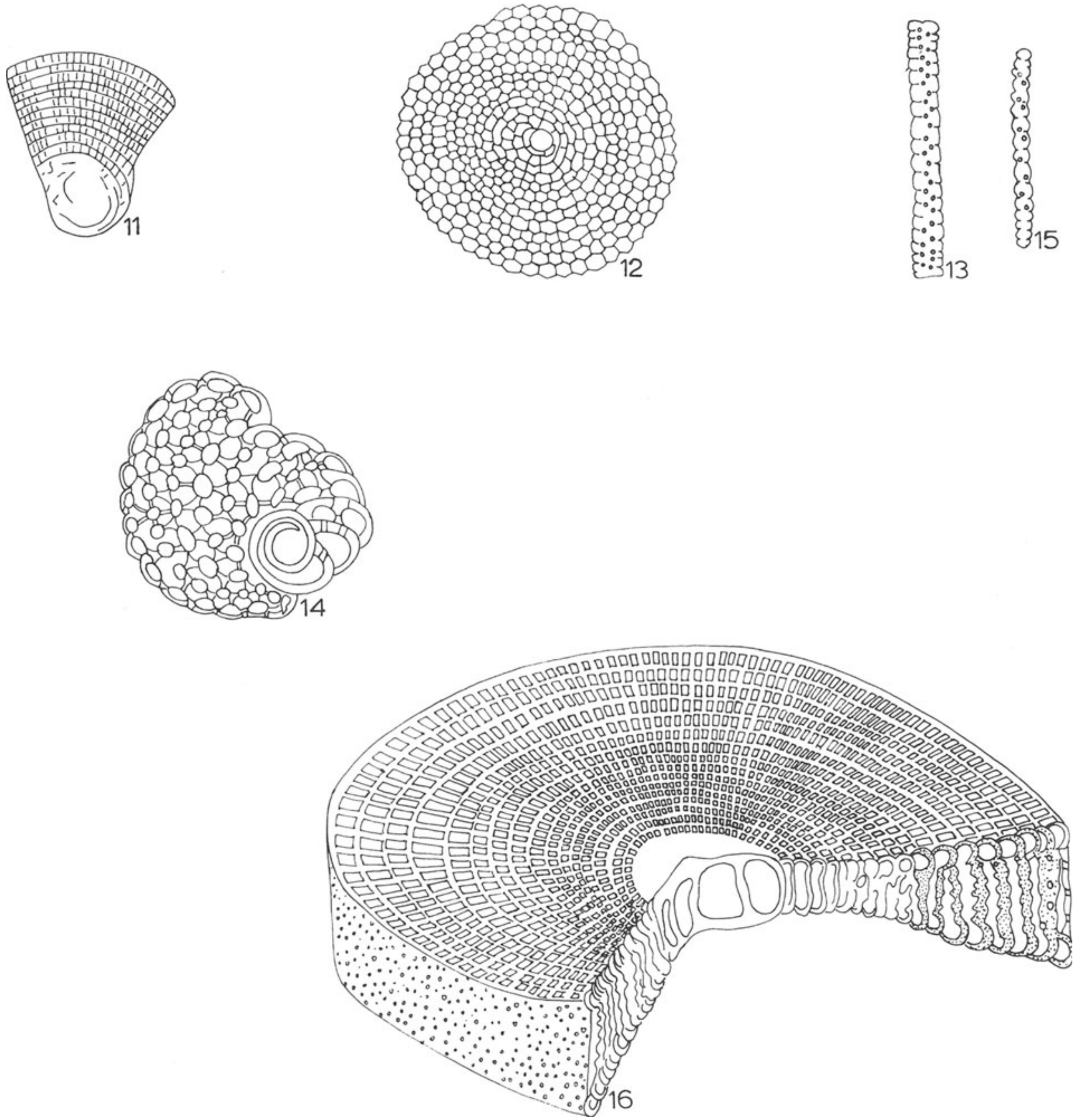
3/4 ***Peneroplis planulatus*** **Fichtel & Moll, after Loeblich & Tappan, 3 side view, 4 apertural view, × 32**

5/6 ***Archaias angulatus*** **(Fichtel & Moll), 5 side view, 6 apertural view, × 21**

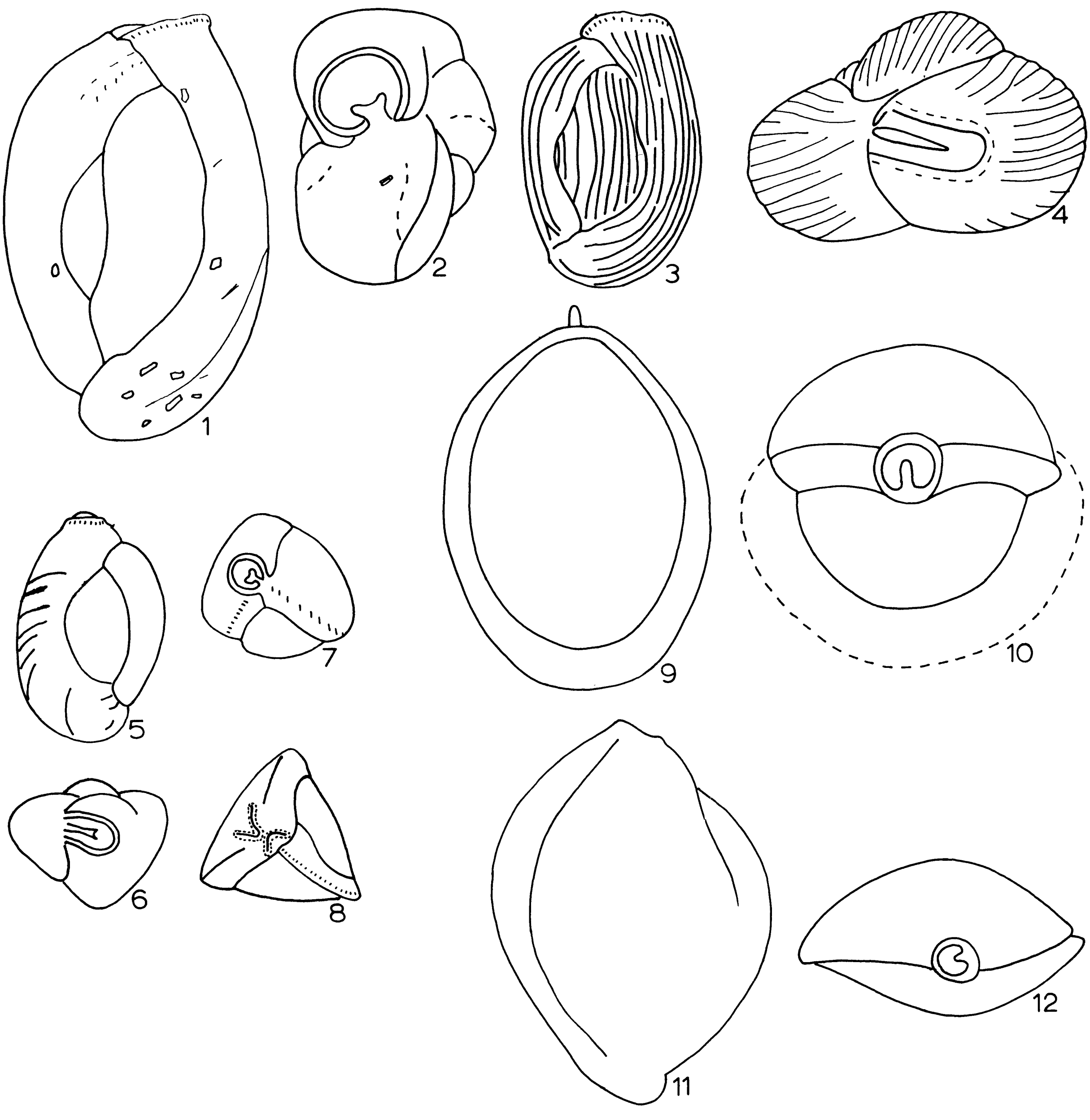
7 ***Archaias angulatus*** **(Fichtel & Moll), median section, after Cushman, irregular pillars giving the appearance of partitions, × 21**

8 – 10 ***Haurania deserti*** **Henson, 8/9 side view and apertural view, 10 equatorial section, × 56**

Key figure 8.11 *(continued)*



11 *Pseudorhipidionina macfadyeni* ? (Henson), side view, × 17
12/13 *Amphisorus hemprichii* Ehrenberg, 12 side view, 13 edge and apertural views, × 11
14/15 *Sorites marginalis* (Lamarck), diag., 14 median section juvenile, × 35, 15 edge and apertural views, × 21
16 *Marginopora vertebralis* Quoy & Gaimard, diag., × 10 with cut-away to show internal tripartite structure, × 63



Key figure 8.12 Miliolacea, Miliolidae

1/2 *'Adelosina' aspera* (d'Orbigny), front view and apertural view, from Haynes, × 70

3/4 *Quinqueloculina ('Lachlanella') bicornis* (Walker & Jacob), front view, × 70, and apertural view, from Haynes, × 84

5/6 *Affinetrina planciana* (d'Orbigny), front view and apertural view, after Luczkowska, × 105

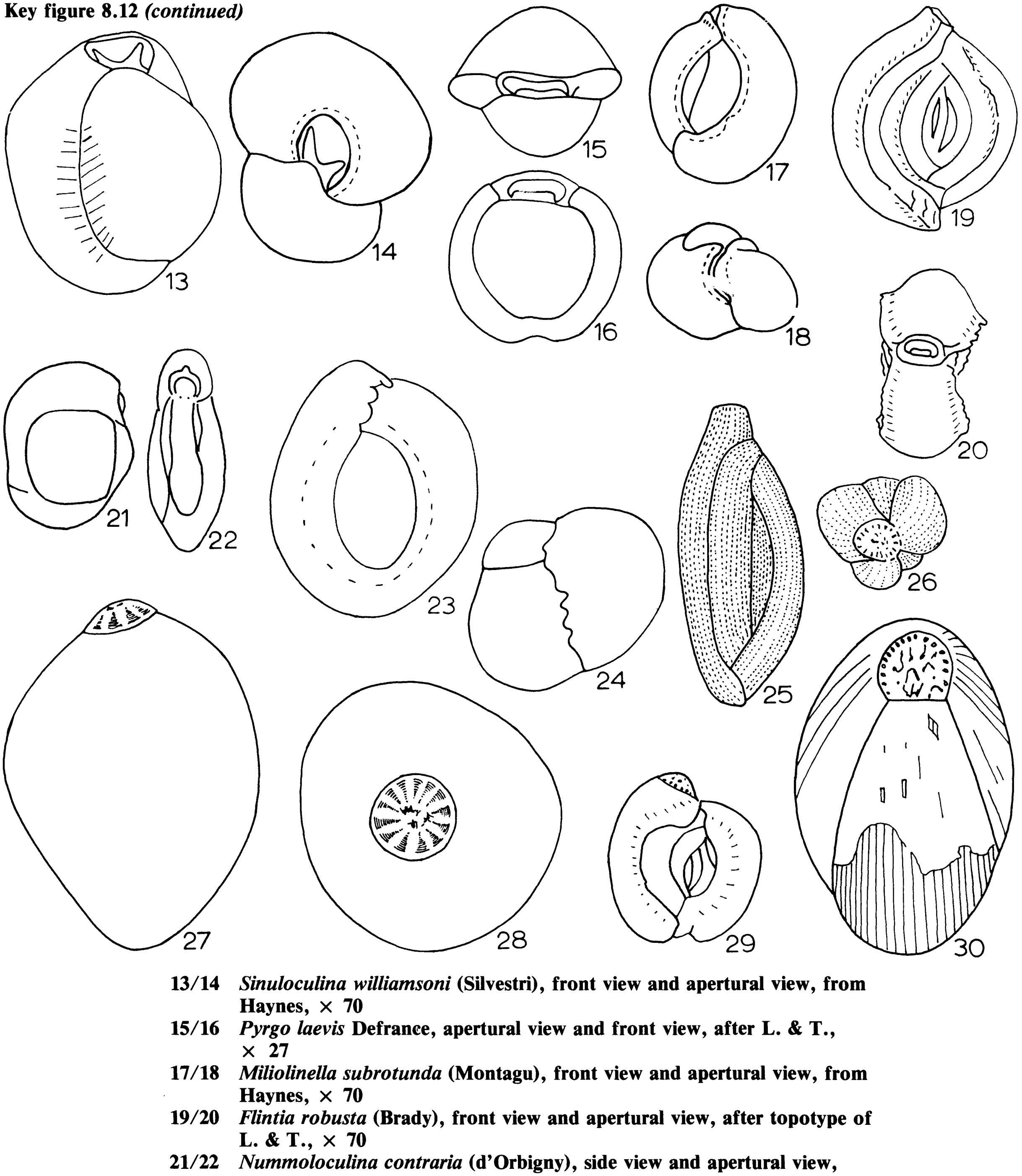
7 *Triloculina trigonula* Lamarck, apertural view, after L. & T., × 21

8 *Cruciloculina triangularis* d'Orbigny, apertural view, after L. & T., × 14

9/10 *Biloculina bulloides* d'Orbigny, front view and apertural view from type figure, no mag.

11/12 *Sigmoilina sigmoidea* (Brady), front view and apertural view, after L. & T., × 63

Key figure 8.12 *(continued)*



13/14 *Sinuloculina williamsoni* **(Silvestri), front view and apertural view, from Haynes, × 70**

15/16 *Pyrgo laevis* **Defrance, apertural view and front view, after L. & T., × 27**

17/18 *Miliolinella subrotunda* **(Montagu), front view and apertural view, from Haynes, × 70**

19/20 *Flintia robusta* **(Brady), front view and apertural view, after topotype of L. & T., × 70**

21/22 *Nummoloculina contraria* **(d'Orbigny), side view and apertural view, after L. & T., × 35**

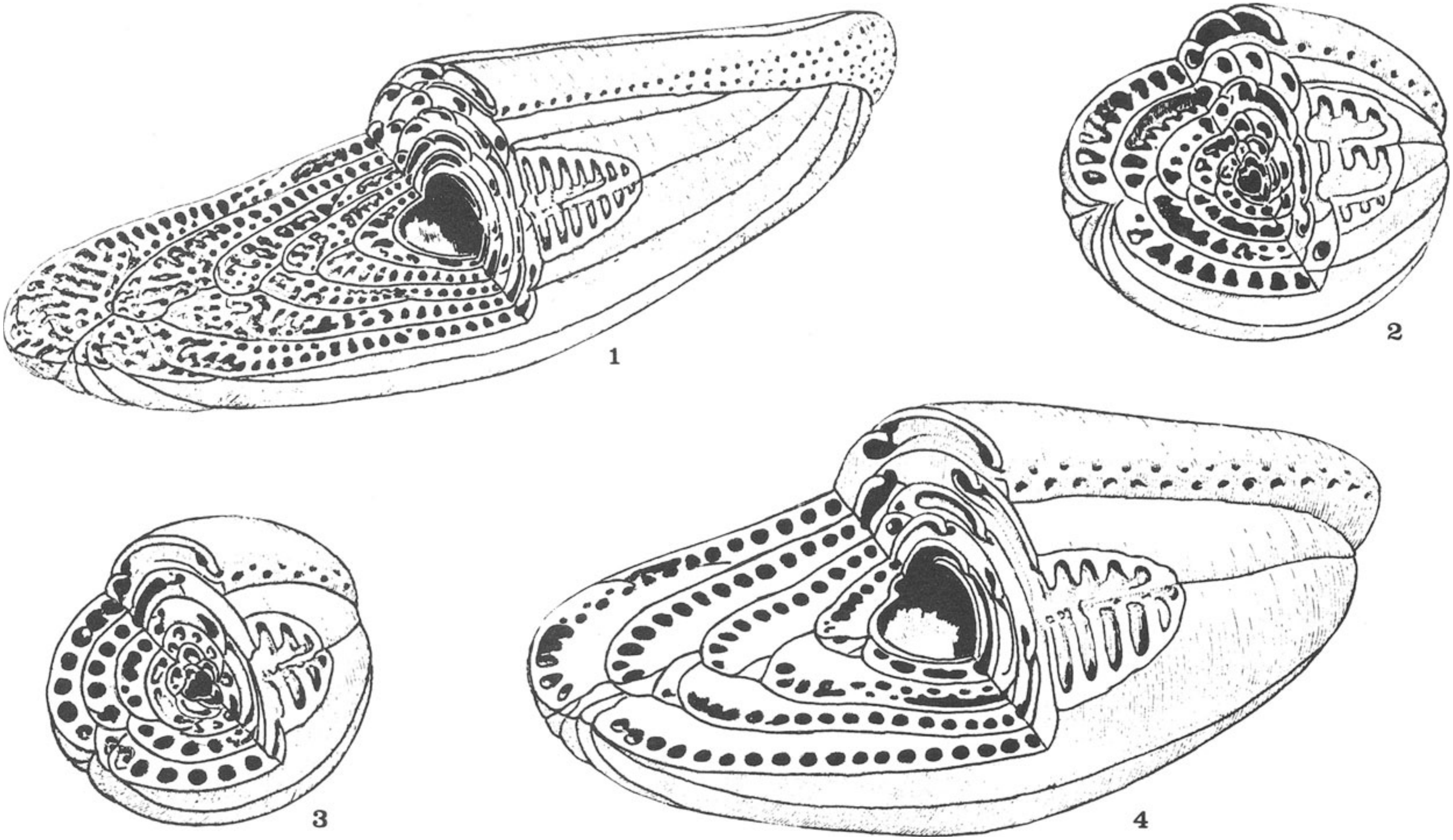
23/24 *Crenetella mira* **Luczkowska, front view and apertural view, type figure, × 210**

25/26 *Miliola saxorum* **(Lamarck), front view and apertural view, after L. & T., × 70**

27/28 *Idalina antiqua* **Schlumberger & Munier-Chalmas, side view and apertural view, after L. & T., × 11**

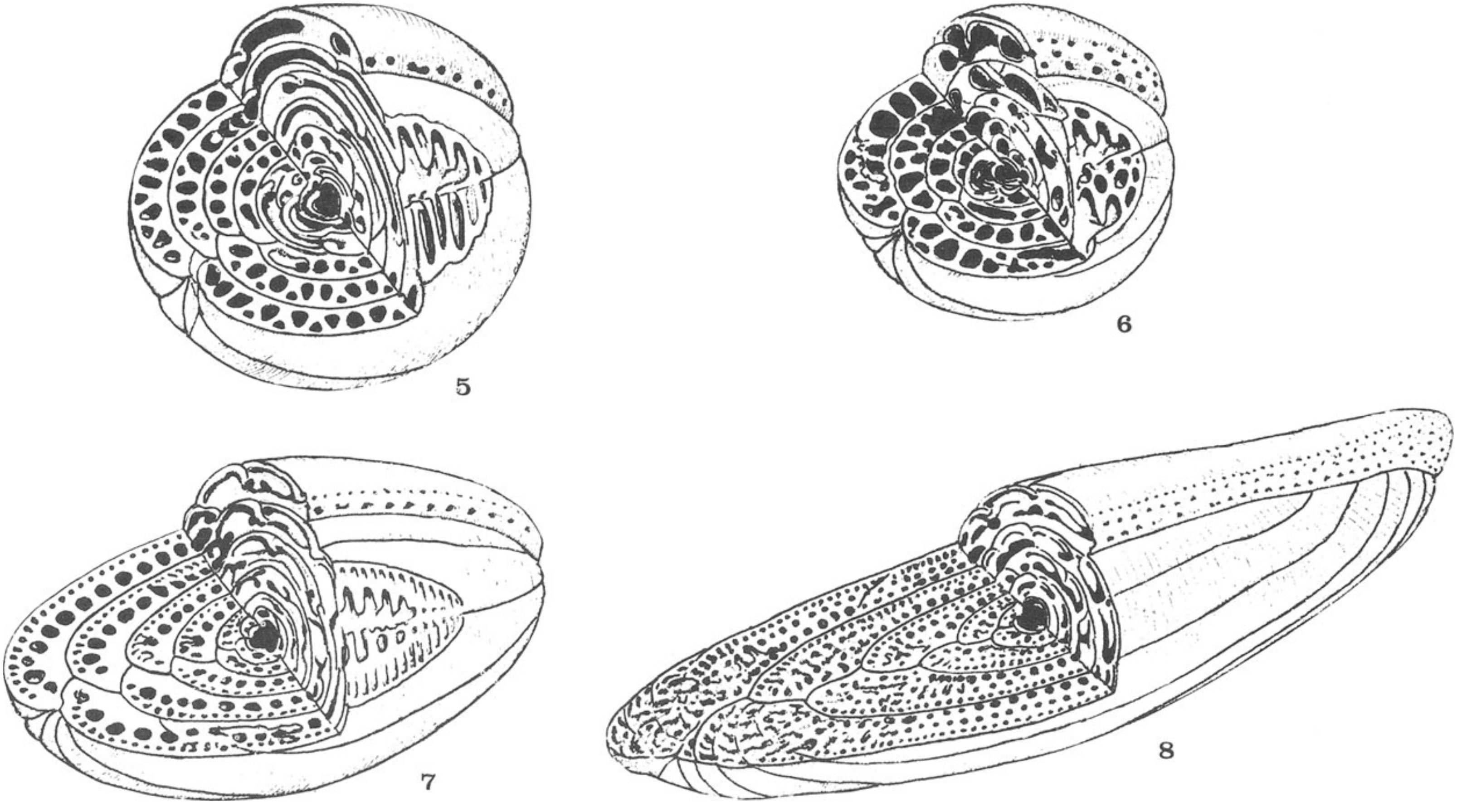
29 *Heterillina guespellensis* **Schlumberger, side view, after L. & T., × 18**

30 *Fabularia ovata* **(de Roissy), front view, after L. & T., × 14**



Key figure 8.13 **Miliolacea, Alveolinidae (all figures diagrammatic after Reichel, with cut-away to show partial axial and median sections)**
1 ***Praealveolina tenuis*** **Reichel, × 45**
2 ***Ovalveolina ovum*** **(d'Orbigny), × 50**
3 ***Glomalveolina primaeva*** **(Reichel), × 55**
4 ***Alveolina schwageri*** **(Checchia), × 55**

Key figure 8.13 *(continued)*



5 *Borelis melo curdica* (Reichel), × 85
6 *Bullalveolina bulloides* (d'Orbigny), × 80
7 *Flosculinella bontangensis* (Rutten), × 60
8 *Alveolinella quoyi* (d'Orbigny), × 45

Chapter 9

The Nodosariida

> Recognition of variable species among the Jurassic Lagenidae (Nodosariidae) is compatible with genetic and evolutionary theory. Moreover, the occurrence of variants is believed to provide important clues to the phylogeny of the group. The occurrence of identical structural types in distinct lineages suggests that many of the described genera of Lagenidae are polyphyletic.
>
> (Cifelli, 1960)

As was explained in chapter 4, the appearance of the lamellar test in the calcareous Foraminifera was an evolutionary event of great significance. This type of construction is light but architecturally strong and allows the addition of continuous external ornament. The possibilities inherent in this wall structure are well shown by the rapid rise of the Nodosariida. They were subordinate to other groups in the Permian but reached a position of extreme dominance in the early Mesozoic, especially in the Jurassic.

Although the Nodosariida range through to the present day, their 'culmination' was in the Jurassic (Barnard, 1950c; Putrya, 1970) and in the late Mesozoic and Cenozoic they again became subordinate to other orders of Foraminifera. Their ecological range was apparently much greater in the early part of their history and they occupied shallower environments prior to the Cretaceous. Since then they have tended to occur mainly in deeper waters. This represents a retreat in the face of competition from other calcareous groups and parallels the history of the agglutinating families discussed in chapter 6. It means that their ecology in the early Mesozoic cannot be interpreted simply by reference to present-day distributions, in the manner so successfully employed with the Miliolida.

A further difficulty is that a large number of genera are founded on Recent material rather than on species from the Mesozoic when the adaptive radiation of the group was at its height. In many cases similar forms have arisen from the same stocks (iterative or repeated evolution). Therefore, many genera are probably polyphyletic and their morphological limits are imprecise. Despite these difficulties this order has proved of great value in Mesozoic stratigraphy.

The wall is monolamellar or multilamellar but the lamellae may be only partially investing (figure 4.5). It is not yet clearly established whether these variations are of taxonomic significance. Attempts to distinguish early Mesozoic forms on the grounds of their supposed microgranular or partially microgranular walls (Norling, 1968, 1972) have proved unsuccessful. As noted earlier, Grønlund and Hansen (1976) have shown that the microgranular layer in Jurassic forms is of diagenetic origin. This supports the previous work of Zobel (1966) and the view that wall structure is a stable feature in the Nodosariida. It is characteristically glassy, radial hyaline and densely perforated with fine pores and no essential change has taken place in composition or structure since at least the Lower Lias.

The Nodosariida are also distinguished by their planispiral to uncoiled and uniserial or polymorphine chamber arrangement. The aperture is terminal in most genera, usually furnished with radiating slits or grooves and may be developed as a full trematophore. A remarkably high proportion of the genera are fully uniserial in this group and external ornament of ribs or costae, umbilical bosses, septal nodes and peripheral keels is commonly developed. In the uniserial forms, in particular, the ornament is generally parallel to the length or axis of the test.

There are no large, complex genera in this group or genera with internal subdivisions. Most species are small but some, particularly in the Cretaceous, reach lengths of more than 1 cm.

CHAMBER FORM AND COILING MODES

The Nodosariida are a relatively small order of Foraminifera, with some 84 genera recognised in the 'Treatise' (Loeblich and Tappan, 1964) but up to a 100 by later workers (Grigelis, 1977). Although they do not include large complex forms, or genera with internal subdivisions, and have remained simple since the Permian, they do exhibit considerable diversity of form. The table of coiling modes (figure 4.3) shows that planispiral to uncoiled (17 per cent) and uniserial (29 per cent) are together the dominant types of arrangement making up just under half of the total. Polymorphine arrangement, where the chambers alternate about a vertical axis, reaches 30 per cent. There are a relatively high number of globular unilocular genera (7 per cent) and irregular, attached forms (10 per cent). Biserial to uniserial arrangement also reaches 7 per cent. The proportion of fully uniserial genera is greater in this order than in any other—almost one-third of the total.

The superfamilies and families are distinguished by these differences in chamber arrangement, together with differences in the form of the aperture.

Nodosariacea

Planispiral or biserial to uncoiled and uniserial genera are included in the superfamily Nodosariacea. The aperture is usually round with radiating marginal slits or becomes a definite closed structure (trematophore) with radiating slits or pores. It may also be a simple, slit-like or oval to round opening.

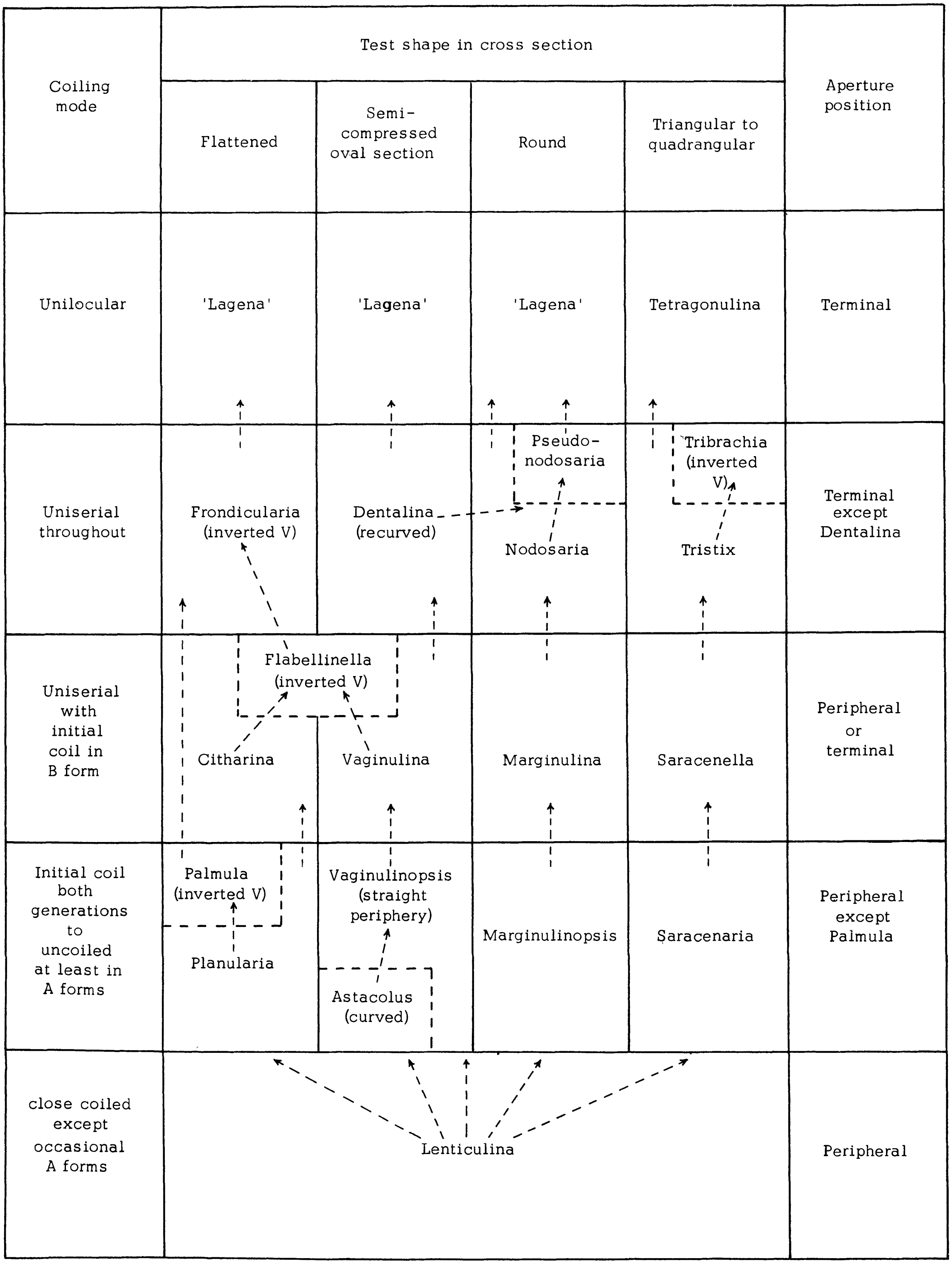
Planispiral to uniserial and unilocular forms are included in the family Nodosariidae, biserial to uniserial forms in the family Plectofrondiculariidae following Montanaro Gallitelli (1957). Planispiral to uniserial genera with simple apertural slit are placed in the Lingulinidae following Grigelis (1977). Coiled forms are not separated from the straight, uniserial genera of the Nodosariidae, as suggested by Putrya (1970), Loeblich and Tappan (1974) and Grigelis (1977) who followed Chapman, Howchin and Parr (1934), see further below. Glaessner (1945, see reprint 1963a) suggested that biserial arrangement in this group simply represented the occurrence of incompletely equitant chambers. The family Plectofrondiculariidae is, however, retained although clearly polyphyletic.

Polymorphinacea

Genera in which the chambers are arranged in an alternating spiral about a longitudinal axis with terminal aperture are included in the superfamily Polymorphinacea. The aperture may have a central opening with marginal, radiating slits but in most cases is fully closed as a trematophore. Genera without internal apertural tube and quinqueloculine to biserial and uniserial are included in the family Polymorphinidae. Triserial to uniserial and unilocular genera with internal tube are included in the family Glandulinidae. A number of the genera show occasional attachment structures, *Webbinella,* and develop fistulose growth over the apertural region with tubular accessory apertures. Similar, bulbous structures occur freely, *Ramulina,* and attached to various substrates, *Bullopora.* These are regarded as form genera, see key figure 9.7.

The major difficulty in distinguishing the genera in both superfamilies is that each family represents a morphological continuum so that the limits have to be arbitrarily fixed. The problem in the Nodosariidae is well illustrated by *Lenticulina* and its allies (key figure 9.6 and figure 9.1). This genus is defined as including species which are compressed planispiral and involute. Species which become uncoiled in the adult are variously grouped as *Astacolus,* if semi-compressed; as *Planularia,* if very compressed; as *Marginulinopsis* if subrounded to round; and as *Saracenaria* if triangular. The aperture remains peripheral, so in the absence of qualitative changes in apertural structure and position, diagnosis is necessarily restricted to these gradational features.

As is to be expected, many species of *Lenticulina* show the incipient development of features which become fixed and diagnostic in more advanced genera. In this sense a single species in the group may show variation of 'generic' as well as specific characters (Barnard, 1950a, 1950b, 1950c, 1960; Adams, 1957; Cifelli, 1960; Gordon, 1966). Thus *Lenticulina* species in the Lower Jurassic may show variants which classed as isolated specimens could be placed as *Astacolus, Planularia,* or with the other subgenera. In the Middle Jurassic, although most species such as *L. quendstedti* are close-coiled, others such as *L. muensteri* and *L. varians* show uncoiled variants. Again, in the Upper Jurassic, *L. muensteri* produced variants that can be placed with *Astacolus, Planularia* or *Marginulinopsis.* These subgenera also intergrade and at certain levels, as in the Upper Lias of Byfield, some specimens of *L. varians* show direct assumption of inverted V-shaped chambers (equitant). It is also claimed (Adams, 1957) that most species of *Planularia* in the Upper Lias are capable of producing equitant chambers. This emphasises the necessity of study-



Coiling mode	Test shape in cross section				Aperture position
	Flattened	Semi-compressed oval section	Round	Triangular to quadrangular	
Unilocular	'Lagena'	'Lagena'	'Lagena'	Tetragonulina	Terminal
Uniserial throughout	Frondicularia (inverted V)	Dentalina (recurved)	Pseudo-nodosaria Nodosaria	Tribrachia (inverted V) Tristix	Terminal except Dentalina
Uniserial with initial coil in B form	Flabellinella (inverted V) Citharina	Vaginulina	Marginulina	Saracenella	Peripheral or terminal
Initial coil both generations to uncoiled at least in A forms	Palmula (inverted V) Planularia	Vaginulinopsis (straight periphery) Astacolus (curved)	Marginulinopsis	Saracenaria	Peripheral except Palmula
close coiled except occasional A forms	Lenticulina				Peripheral

Figure 9.1 **Genera of Nodosariidae arranged in morphological series showing uncoiling from *Lenticulina***

ing the range of variability in each species and within each evolving group or plexus, as recommended by Barnard (1950a).

It is also clear that the genera cannot be narrowly interpreted simply on the range of form shown by the genoholotypes. A particular difficulty occurs when a species appears to fall midway between two genera, as in the case of *Astacolus platypleura* from the Lower Tertiary (Haynes, 1958a). In this species the A forms show a consistent tendency to uncoil in the adult part, while the rare B forms are close-coiled. On this basis it was included in *Astacolus,* although the type species for that genus, *A. crepidula,* is uncoiled in both generations.

This Thanetian example shows that the potential for high variability was retained by *Lenticulina* throughout the Mesozoic and into the Tertiary. The same variations were produced many times, making it very likely that many of the genera are polyphyletic. Attempts have been made to subdivide some of the genera on time of appearance; thus planispiral to equitant species in the Jurassic were formerly distinguished from *Palmula* in the Cretaceous as *Falsopalmula.* But as there is no real morphological difference this name has been largely abandoned.

When classification at family levels depends upon apertural characters, particular care is necessary in the interpretation of fossil material, especially from the early Mesozoic. Terminal apertures and trematophores are open to damage or loss. In most cases they appear to have been resorbed during growth and broken specimens merely show the foramen. Undoubtedly, a large number of published figures purporting to show the aperture are actually of broken specimens. It is still uncertain how far the differences in radiate apertures, discussed by Barnard (1950c) and more readily detectable by SEM (Norling, 1968, 1972; Murray, 1971b; Haynes *et al.* 1973), can contribute to classification above the species level, although Haman (1978) considers the presence of a porous trematophore of more significance in the *Lenticulina* group than partial uncoiling and shape in cross-section. The internal tube in the Glandulinidae is often difficult to detect in fossil material and specimens may require surgery to reveal its presence.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

The Nodosariida arose in the Permian, remained rare through the early Triassic but burgeoned to reach maximum numbers in the late Triassic and Jurassic. Thereafter the order shows relative decline, although both superfamilies continue to show diversification through the Cretaceous and Cenozoic. They are closely allied in wall structure and apertural form and it might be thought that the phylogenetic relationships of the families would be well understood. This is not so, because the origins of the Nodosariacea and Polymorphinacea are respectively in the Permian and early Triassic where they are localised, often recrystallised and poorly known. The problem is also, to some extent, further confused by the wealth of material from the Jurassic with the evidence it affords of the rise of polyphyletic genera (heterochronous homeomorphs) from the same basic stocks at different times (iterative evolution) as well as from different stocks by convergence. This has meant that different workers have drawn different conclusions from the same material.

The Nodosariidae were first to appear and it is this family that dominates the Jurassic. As shown by figure 9.1, the genera can be arranged in a morphological series, and if the principle of recapitulation is employed (the biogenetic law) this can be interpreted as an evolutionary series showing various lines of uncoiling from *Lenticulina.* This interpretation was followed by Galloway (1933), Cushman (1948) and Glaessner (1945, 1963a). On the other hand, Chapman, Howchin and Parr (1934), impressed by the apparent lack of close-coiled forms in the Permian, whereas *Nodosaria, Dentalina* and *Frondicularia* are present, decided that the ancestor of the Nodosariidae could not have been close-coiled. Following this line of reasoning the close-coiled and partly uncoiled forms were put into a separate subfamily, the Lenticulininae (Chapman, Parr and Collins, 1934). Although *Lenticulina* has since been discovered in the Permian by Crespin (1958) this view has been followed by Fursenko (1959b), Brotzen (1963), Putrya (1970) and finally Grigelis (1977), who has raised the subfamily to family rank. The ancestor of the uniserial nodosariids is considered to have been the microgranular, uniserial *Nodosinella,* while *Lenticulina* is considered to have arisen from a coiled member of the Endothyridae such as *Robuloides.* These views were endorsed by Loeblich and Tappan (1974) with a later amendment by Tappan (1976) proposing that the coiled forms were a later offshoot from the uniserial forms. Grigelis has gone further and considers that *Dentalina* and *Nodosaria* arose separately from the Nodosinellidae, while *Lenticulina* and *Astacolus* also arose separately from the Endothyridae. *Vaginulinopsis* and *Marginu-*

linopsis are considered to have arisen among the uniserial genera by proterogenesis.

In contrast to these views, the opinion of the workers who have made detailed studies on the British Jurassic, especially Adams (1957), Barnard (1960), Cifelli (1960), Gordon (1966), Johnson (1975) and Copestake (1978), is that *Lenticulina* shows a persistent tendency to uncoil. As already explained, variants in these primitive stocks show the incipient development of later genera and there is a clear gradation towards complete uncoiling.

The attempt to demonstrate a gradational change in wall structure between late members of the Fusulinida and the uniserial Nodosariida has broken down while, at the same time, the presence of *Lenticulina* has been demonstrated in the Permian. Invoking the principle of 'Ockham's razor', that the simplest hypothesis that will cover the known facts is to be preferred, it seems reasonable to return to the idea that uniserial genera have arisen from ancestral *Lenticulina* stocks at various times, including the Permian. Further studies are required to demonstrate a possible connection with Upper Palaeozoic genera such as *Robuloides* and *Eocristellaria,* particularly of wall structure on good material. Possibly these genera should be transferred to the Archaediscina (as interpreted herein).

As is shown by the diagram (figure 9.1), four main lines of development can be distinguished within the Nodosariidae according to whether the test cross-section becomes flattened, oval, round or triangular. There is a general tendency for the aperture to become terminal as the test uncoils and inverted V-shaped chambers appear in different lines, particularly in compressed genera but also in the triangular group. These trends show a remarkable parallelism with those already described in the Astrorhizida and discussed in chapter 4. They may represent adaptations to feeding at the sediment/water interface with the uniserial genera becoming fully infaunal in soft sediments and fluid muds. The lanceolate and palmate forms may have glided over the surface, while species with truncate and enlarged apertural faces may have lived upright on the sediment. The presence of a grid-like trematophore is consistent with this idea, as is the general tendency to longitudinal ornament, the strength of the ribs or costae being related to different sediment types. *Lenticulina* was probably less specialized, living as a vagrant surface feeder on a variety of substrates. It appears to have retained its generic variability over a long period, giving rise to the more specialised uncoiled forms when environmental conditions were favourable, Barnard (1950b, 1960).

The Lingulinidae range from the Permian to the Recent and the abundance of the uniserial *Lingulina* in the Permian has been stressed by those workers favouring an independent origin for the uniserial nodosariids from *Nodosinella.* However, many Permian records of *Lingulina* actually refer to *Lunucammina* (= *Geinitzina* of authors). No evidence of a gradation between these two genera exists. Because close-coiled and partially uncoiled lingulinids, *Ellipsocristellaria* and *Lingulinopsis,* are known from the Cretaceous onwards, it seems more likely that *Lingulina* derives from an ancestor near the primitive Permian *Lenticulina* stock, with 'robuline' apertural slit (Galloway, 1933). *Lingulonodosaria* approaches *Nodosaria* in form as the chambers become rounded and less embracing. *'Nodosaria'* species with simple oval to round aperture may have arisen by this route. Unilocular representatives of this family, *Rimulina,* are only known from the Recent.

The Plectofrondiculariidae are a polyphyletic group that may have arisen from different members of the Nodosariidae at different times: *Kyphopyxa* from *Vaginulina* in the Cretaceous, leading to *Plectofrondicularia* and the uniserial *Amphimorphina* in the Palaeogene and *Dyofrondicularia* from *Frondicularia* in the Neogene. Fully biserial representatives, like *Lankesterina,* differ from biserial polymorphinids in showing no trace of a guttuline or sigmoid origin.

Eoguttulina, with its simple spiral of globular chambers, which occurs in the Triassic is regarded as the ancestral member of the Polymorphinacea and Cushman and Ozawa (1930) consider it was 'undoubtedly derived from some coiled member of the "Lagenidae" such as *Marginulina* or *Vaginulina* by introduction of a spiral arrangement of the chambers'. *Eoguttulina* apparently gave rise to the partially biserial *Glandulopleurostomella,* the fully biserial *Pyrulinoides* and the biserial/uniserial *Sagoplecta,* as well as to quinqueloculine *Guttulina* and quinqueloculine/triloculine *Globulina* before the end of the Triassic. All of these genera have been recorded in the Trias (Tappan, 1951; Zaninetti, 1976), but lack of information means that the apparent morphological series cannot be proven to be a definite evolutionary line. *Globulina* apparently gave rise to *Pyrulina* and *Guttulina* gave rise to *Pseudopolymorphina* and *Sigmomorphina* in the Jurassic, with the further development of *Polymorphina* and *Sigmoidella* in the early Tertiary. There is thus a general tendency towards reduction of chambers in the coil and uniserial growth, or the appearance of flattened or sigmoid biserial forms.

The early history of the Glandulinidae can only be understood when the internal apertural characters of early Mesozoic forms are better known. But triloculine/biserial *Dainita* occurs in the Cretaceous and triloculine/uniserial *Barnardina* in the Palaeocene, probably giving rise to biserial/uniserial *Glandulina* in the late Tertiary. The occurrence of triserial genera in the Recent, such as *Siphoglobulina* and *Globulotuba,* indicates that this group may derive from a Jurassic ancestor similar to *Globulina* but which had an internal tube. Support for this idea is given by the presence of a form very similar to *Globulina gibba,* but with internal tube, in the Thanetian (Palaeocene) of England (Haynes, 1958b). The A. forms of *Barnardina* and *Glandulina* show reduction to two chambers only, so unilocular *Oolina* is probably polyphyletic and may derive from both Mesozoic and Cenozoic stocks.

The aperture is terminal in all polymorphinids, and taken with the tendency towards chamber reduction may indicate that this superfamily was also adapted to life on soft substrates at the sediment/water interface. Uniserial genera may have been infaunal, while flattened biserial forms glided over the surface. Longitudinal ornament is again common and some species of *Polymorphina* show strong ribs (often paired) down the central line, like *Frondicularia* and *Lingulina.* It is even possible that some species of *Sigmomorphina,* for instance, *S. torta,* could screw their way through fluid sediments.

STRATIGRAPHICAL USE OF THE NODOSARIIDA

Most families and genera of the Nodosariida are long ranging, and application in stratigraphy is mainly at the species level. Many species are of quite short range especially among advanced Nodosariidae and, indeed, Putrya (1970) went so far as to say that 'among Lenticulinidae there are no long-lived species, their vertical distribution is usually limited by a stage and sometimes even by a zone'. The group has been applied most successfully in the Jurassic and to a lesser extent in the Cretaceous, more especially in the Lower Cretaceous.

Attention was paid to the Lower Jurassic or Lias from early in the nineteenth century by European workers, by Strickland (1846), Jones (1853), Jones and Parker (1860), Brady (1867), Blake (1876a), Crick and Sherborn (1891, 1892) in England, and by Bornemann (1854) in Germany and Terquem (1858, 1867) in France. This early phase is interesting as it illustrates very well the split between the 'English School' and the 'Continental School', discussed in chapter 5. Some species in England were equated with Recent forms while on the Continent, especially in the papers by Terquem, some taxa were excessively split while others were interpreted to include disparate forms, so that species included 'a miscellany of heterogeneous specimens' (Cifelli, 1960). The middle way between these extremes was not taken until the twentieth century, with the development of the modern species concept and examination of the variation within the evolving plexus, as advocated by Bartenstein (1948b), Barnard (1950a, 1972), Adams (1957) and Bhalla and Abbas (1975) and applied particularly to *Lenticulina.*

Detailed examination of the Middle and Upper Jurassic did not get under way until the middle years of this century, although pioneer work was done on the Middle Jurassic by Terquem (1868, 1870) and on the Kimmeridgian (Hartwell Clay) by Neaverson (1921). Research has now gone ahead rapidly, especially in England (Barnard, 1952, 1953; Cifelli, 1959; Cordey, 1962; Gordon, 1962, 1965, 1966, 1967). Other important studies have been made in Germany (Lutze, 1960; Seibold and Seibold, 1960), Poland (Bielecka and Pozaryski, 1954; Bielecka, 1960; Kopik, 1969) and Russia (Kaptarenko-Chernousova *et al.,* 1963), while the faunas of Western and Eastern Europe have been compared by Groiss (1976). In North America the faunas of the Western Interior have been studied by Loeblich and Tappan (1950a, 1950b) and Wall (1960), and those in Alaska by Tappan (1955). Work has also been done on the Oxfordian sediments of the East Atlantic (Kuznetsova and Seibold, 1977). These are the oldest deposits detected in JOIDES cores in the Atlantic Basin and provide significant information regarding its development.

The Nodosariida, in particular the Nodosariidae, are commonly the dominant element in these faunas, sometimes to the almost complete exclusion of other groups. The Polymorphinacea occur more rarely. The main genera of the Nodosariidae occur throughout but *Citharina* does not appear before the Upper Lias. *Lingulina* is particularly prominent in the late Trias and Lias and *Lenticulina* in the Middle and Upper Jurassic. Some species are extremely widespread, thus *Lenticulina tricarinella,* which ranges through the Bathonian – Oxfordian interval, is known throughout Europe and also occurs in Sinai (Said and Barakat, 1958) and Kutch (Bhalla and Abbas, 1976, 1978).

The most detailed zonation on the basis of the Nodosariidae has been achieved in the Lias and for this reason it is appropriate to examine the work carried out on that part of the succession more closely, especially since the proving of 1305 m of Liassic strata in the Mochras Borehole, N. Wales (1967 – 69) with a complete, continuously cored succession of ammonite zones and subzones, has allowed the establishment of a key section for correlation with Europe and N. America (Johnson, 1975, 1976; Copestake, 1978; Copestake and Johnson, 1981).

The first zonal schemes based on Foraminifera for the Lias were produced in Germany by Bartenstein and Brand (1937) and in England by Barnard (1950c). These attempts were followed by those of Bang for Denmark (1968, 1971, 1972) and of Norling for Sweden (1972). A modified version of the overall zonal scheme for the exceptionally thick sequence in North Wales is reproduced in the table in figure 9.2. Ten zones (excluding subzones) are recognised, equivalent to 20 ammonite zones, so each foram zone is equal to about two ammonite zones. Eight of the zone name forams are nodosariids, as are the great majority of the subsidiary index forms. The most important of these are shown in the list on the right-hand side of the chart. It will be seen that a wide spectrum of the genera in the family is represented. See also plate 11.

As in most Jurassic sections, nodosariids tend to dominate at most horizons and usually make up more than 50 per cent of the total fauna, except in the Pliensbachian and the Lower Toarcian. At a number of horizons this group makes up more than 90 per cent of the total. Specimens tend to be small in the Lower Lias and are found mainly in the 200 mesh sieve (75 μm) but increase in size in the Middle Lias (Upper Pliensbachian) and Upper Lias (Toarcian). The table brings out very well the importance of *Lingulina,* especially in the Lower and Middle Lias, and the dramatic entry of large species of *Citharina* at the beginning of the Upper Lias.

The table also illustrates some of the problems faced by the stratigrapher in the attempt to use fossils in zonal biostratigraphy. The zones are erected on the basis of the total vertical range of a particular distinctive index species (local range zone) or on their period of maximum abundance (acme zone). As can be seen, a number of the zones recognised are a combination of both. In each case the zonal index forms are supplemented by a number of species with total vertical ranges or period of peak abundance confined within the zone limits. Although not shown in the table, a number of other species of longer range overlap in particular combinations and help to give the zones their special identity (the zones are therefore also assemblage zones). Also of value in the recognition of the zones are the horizons of first appearance and disapearance of certain species (first and last occurrences).

A major difficulty in using the zones for correlation with Liassic rocks elsewhere is that the local range may be curtailed by environmental influences and, thus, only partially represent the true life range from evolutionary appearance to extinction (biozone). For instance, *Planularia inaequistriata* has a longer range in Denmark and Sweden than in Mochras, while *Nodosaria issleri* has a slightly longer range in Germany than in Mochras or Denmark. These ranges are being measured against the ammonite zones but we must remember that, although based on a rapidly evolving pelagic group, these too, must be time transgressive to a degree when traced over long distances (homotaxial). However, despite these difficulties, the foraminiferal zones are recognisable in many European sections and occur in the same order in different countries. This means they probably do reflect evolutionary events.

The short ranges of many of the species, well within the limits of the stages, goes some way towards justifying Putrya's proud boast concerning their stratigraphical utility. But it has to be admitted that many are 'empirical index fossils' in the sense of Glaessner (1966) and as has been explained in chapter 5, the most accurate biozones (and hence the most refined biostratigraphy) are those based upon an evolving lineage (or species plexus) where it is possible to pinpoint the appearance and disappearance of the successive species (rational index fossils).

Progressive evolution is shown in the Lias by a number of species (Barnard, 1956, 1957, 1963b; Nørvang, 1957; Copestake, 1978) and in particular by the *Lingulina tenera* plexus. This is the most abundant species group of all in the Lower and Middle Lias and the value of the short-ranged variants (figure 9.2) is enhanced by recognition of their place within the evolving plexus. The main trends involve changes in ornament and shape and length of the test.

Lingulina tenera tenera Bornemann is distinguished by bearing two, main, longitudinal ribs either side of a median sulcus and is keeled. Range: Late Trias. – L. Toarcian.

STAGES		AMMONITE ZONES	FORAMINIFER ZONES	ADDITIONAL INDEX SPECIES NODOSARIIDAE
TOARCIAN	Upper	levesquei	Palmula tenuistriata* & Nodosaria regularis robusta	Marginulina breviformis Saracenella mochrasensis Citharina colliezi* Lenticulina orbignyi*
		thouarense		
	Lower	variabilis	Reinholdella macfadyeni	Frondicularia terquemi muelensis (last) Lenticulina orbignyi ✪ Lingulina tenera tenera (last)
		bifrons		
		falciferum	Nubeculinella tibia	Citharina colliezi ✪ C. frankei ✪ C. saggitiformis ✪
		tenuicostatum	Reinholdella dreheri* Reinholdella pachyderma*	Citharina mochrasensis ✪
PLIENSBACHIAN	Upper	spinatum	Saracenaria sublaevis sublaevis	Citharina clathrata ✪ F. terquemi bicostata* Vaginulina proxima ✪ Marginulina ex gr. prima* Dentalina gladiiformis* D. tenuistriata* Vaginulina listi*
		margaritatus	Berthelinia pictonica	Lingulina gottingensis L. longiscata cf. alpha Marginulina picturata Nodosaria kuhni Lingulina tenera occidentalis* & pupa* L. testudinaria Marginulina prima interrupta ✪ Frondicularia terquemi muelensis*
	Lower	davoei		
		ibex		
		jamesoni		
SINEMURIAN	Upper	raricostatum	Dentalina matutina* & Nodosaria issleri	Saracenaria sublaevis hannoverana Saracenella trigona Vaginulinopsis erzingensis Lenticulina muensteri gr.* Pseudonodosaria vulgata*
		oxynotum		
		obtusum		
	Lower	turneri	Reinholdella matutina* & Neobulimina bangae	Astacolus semireticulata Lingulina tenera subprismatica* Marginulina obliquecostulata Nodosaria columnaris* ✪ Planularia aff. pickettyi P. pulchra Vaginulina listi* ✪
		semicostatum		
		bucklandi		
HETTANGIAN		angulata	Planularia inaequistriata* & Lingulina tenera substriata*	Neoflabellina cf. ferruginea Saracenaria segmentata Vaginulina curva* ✪
		liasicus	Reinholdella planiconvexa* & Lingulina tenera striata	Frondicularia terquemi barnardi ✪
		planorbis		
		Range zones except where marked : acme* first occurrence ✪		

Figure 9.2 Zonal scheme for the Mochras Lias, based on Copestake and Johnson (1980). Note importance of nodosariids and *Reinholdella*

L. tenera form E. Barnard, has a weak median rib also. Range: Lowermost Sinemurian

L. tenera tenuistriata (Nørvang), has additional longitudinal striae. Range: Rhaetic – Pliensbachian.

L. tenera striata (Blake), has irregular ribs of equal strength. Range: L. Hettangian.

L. tenera substriata (Nørvang), has wavy ribs with 2 relatively stronger. Range: Hettangian.

L. tenera pupa (Terquem), has strong inter-rib striae, no keel and constricted (pupate) later chambers. Range: Sinemurian to U. Jur.

L. tenera form H. Barnard, flattened with fine discontinuous striae. Range: U. Sinemurian.

- *L. tenera* H. Copestake, convergent striae. Range: U. Sinemurian to Pliensbachian?
- *L. tenera subprismatica* Franke, elongated with hexagonal cross-section and basal spine. Range: Upper Sinemurian to Lower Pliensbachian.
- *L. tenera occidentalis* (Berthelin), flattened with raised sutures between marginal ribs. Range: from just below Pliensbachian to lowermost Toarcian.

Barnard considered that *L. tenera tenera* was the ancestral stock giving rise to all the other subspecies through the Lower Lias, while Nørvang considered *L. tenera striata* to be the ancestral form. However, *L. tenera tenuistriata* is present in the lowermost Hettangian at Mochras and together with *L. tenera tenera* is also known in the Rhaetic (Kristan-Tollmann, 1964), apparently prior to the appearance of *L. tenera striata* and *L. tenera substriata* in the Hettangian. Copestake therefore considers *L. tenera tenera* and *L. tenera tenuistriata* as jointly comprising a central interbreeding stock from which the other subspecies diverge. The time of first appearance and ranges of these forms in Mochras are closely matched in the Stowell Park borehole, Gloucestershire, studied by Barnard.

The Liassic foraminiferal faunas of N. W. Europe show remarkable uniformity when compared with those of Mochras, especially in the Lower Lias. As is to be expected, other sections in Britain show high percentages of species in common. Thus 42 of the 47 species recorded by Barnard (1950a) from the Lower Lias of Dorset, some 90 per cent, also occur at Mochras. There are similar high 'co-occurrence' figures of 80 per cent for the Belemnite Marls of Dorset (davoei zone) taken alone (MacFadyen, 1941); 80 per cent for the Lower Lias of Yorkshire (Blake, 1876a) and 100 per cent for the Stowell Park borehole in Gloucestershire. There is less similarity in the Middle and Upper Lias: S. W. Britain (Brady, 1876), 40 per cent; Bristol Channel (Banner *et al.*, 1971), 57 per cent. For the Lower Toarcian alone the figures are 59 per cent for Northamptonshire (Barnard, 1950b) and 40 per cent for Lincolnshire (Adams, 1955).

The co-occurrence figures for the Paris Basin (Bizon and Oertli, 1961) are also particularly high and reach 100 per cent in the Lower Lias in the north-eastern part of the basin and the Ardenne (Cousin *et al.*, 1961). There is a fall in the Middle Lias, 43 – 57 per cent, and a rise in the Upper Lias, 50 – 100 per cent in all parts of the basin.

A very considerable amount of work has been done on the Liassic of Germany (Franke, 1936; Bartenstein and Brandt, 1937; Pietrzenuk, 1961; Klinger, 1962; Brouwer, 1969). Of the 162 species recorded in the Lower Lias by Bartenstein and Brandt, 139 were recovered in Mochras, 85 per cent. An even higher co-occurrence marks the Lower Lias of East Germany studied by Pietrzenuk, 90 per cent, where, incidentally, the numbers of Nodosariidae also range between 50 and 90 per cent. Values again fall to between 25 and 46 per cent in the Middle Lias but rise to a maximum of 61 per cent in the Upper Lias. Despite the southerly position of Austria, co-occurrence values there for the Lower Lias reach 64 per cent (Fuchs, 1970).

Values are high for Denmark (Nørvang, 1957; Bang, 1971, 1972), reaching 93 per cent in the Lower Lias, falling to between 40 and 60 per cent in the Middle Lias. As might be expected, values show a fall in Sweden (Norling, 1972) with 72 per cent in the Lower Lias, 36 per cent in the Middle Lias and 48 per cent in the Upper Lias. Traced through Poland (Kopik, 1969; Dadlez, 1969) into Russia (Gerke, 1957, 1961), there is a further marked fall and only 21 per cent of Middle Lias and 8 per cent of Upper Lias Foraminifera are in common. Remarkably, the Alaskan faunas described by Tappan (1955) are much nearer in composition to those of Mochras and some show the same ranges: 63 per cent co-occurrence in the Lower Lias, 25 per cent in the Middle Lias and 46 per cent in the lower part of the Upper Lias. All the species reported by Gradstein (1976, 1978) from the Lower and Middle Lias of the Grand Banks area of Canada occur in Mochras, an indication of the close proximity of these areas prior to the opening of the Atlantic.

Outside this northern realm, co-occurrence falls to low levels but it is noteworthy that even in Sicily (Barbieri, 1964), within the Tethyan Province of Gordon (1974), 46 out of 59 species are in common, 77 per cent, and *Saracenaria sublaevis*, a prominent boreal index species, is also present.

The Nodosariidae continue as abundant forms in the early stages of the Cretaceous (Chapman, 1894; Sherlock, 1914) and large species of *Vaginulina* and *Frondicularia* are typical of the Gault (Albian) of N. W. Europe (Reuss, 1862b; Chapman, 1891 – 98; Khan, 1950, 1952; Price, 1977). Price demonstrates the importance of the first appearances of many species in recognition of his zones, especially in the Lower and Middle Albian. One-third of the benthonic foraminiferal species that are useful as index fossils world wide, in both onshore and offshore L. Cretaceous sections, are members of the Nodosariidae (Bartenstein, 1979).

Some species are very wide ranging, as in the Jurassic. A particular example is *Lenticulina nodosa* which appears at the Jurassic/Cretaceous boundary and reaches the Cenomanian. It has a worldwide distribution that corresponds very well with the pre-drift positions of Africa and S. America, occurring all round the borders of the former landmass but not in Western Africa or eastern S. America (Bartenstein, 1974; Aubert and Bartenstein, 1976).

Despite the relative decline in the Upper Cretaceous the order shows continued diversification (Reuss, 1845–46, 1851, 1860; Marie, 1941; Cushman, 1946; Frizzell, 1954). The work of Krystyna Pozaryska (1957) on the chalk of Poland shows particularly well (her text fig. 1) how all the main genera show continuous expansion with an increase in abundance and diversity from the Cenomanian through the Senonian to reach a peak in the late Maastrichtian. There is then a dramatic fall in the numbers, with the extinction of most species, coincident with the great, end-Maastrichtian regression and the worldwide stratigraphical break at the Mesozoic/Tertiary boundary.

Although the relative decline continued in the Tertiary, the ancestral *Lenticulina* stock retained its vigour in the Palaeogene. Important index species include *Astacolus platypleura* in the Palaeocene and *Astacolus fragaria* in the Eocene of N. W. Europe. *Vaginulina robusta* is another Palaeocene index form found in N. America, N. W. Europe and in the Tethyan region.

ECOLOGY

The Nodosariida are best developed at depths between 50 and 500 fathoms in tropical regions at present and also occur down to the CCD on the abyssal plains (Brady, 1884; Cushman, 1913, 1923; Norton, 1930; Parker, 1948; Lowman, 1949). In contrast, there is a general consensus (following Barnard, 1950c) that in the Jurassic they reached their maximum diversity in depths equivalent to those prevailing on the middle and inner shelf today. Thus Wall (1960) found that nodosariid dominated assemblages in the Middle and Upper Jurassic of Saskatchewan were best interpreted as middle to inner neritic and normal or nearly normal marine. The polymorphinids possibly represented low salinites. Bielecka and Pozaryski (1954) found that nodosariids were rare in extreme shallow water and in limestones such as oolites and more numerous in deeper water in the Upper Jurassic of Poland. Similarly, Brooke and Braun (1972) interpreted diverse nodosariid assemblages as middle neritic and low diversity, nodosariid assemblages as inner neritic. Both Gordon (1970) and Scheibnerova (1971a, 1971b) consider these assemblages represent shallow, land-bordered epicontinental seas.

As was pointed out in chapter 6, in discussion of the ecology of agglutinating Foraminifera, it is difficult to go beyond these generalisations when direct comparison with Recent species is impossible. Knowledge of the ecology of particular species (autecology) in this case depends upon careful study of the sediment and associated biota and quantitative techniques of assessment of the total foraminiferal fauna.

An attempt to measure a depth succession in the Lias on the basis of pairs of species (identified by chi^2 test, Kendall and Stuart, 1961) has been made by Brouwer (1969). His list, here much abbreviated, includes:

Shallow or brackish	*Eoguttulina liassica/ Astacolus stillus* *Lingulina tenera/Eoguttulina liassica*
Open marine near shore	*Lingulina tenera/A. stillus* *Astacolus primus/L. tenera*
Open marine	*Marginulina prima/L. tenera* *Brizalina liassica/M. prima*
Most open marine (deepest)	*Reinholdella/B. liassica* *Lenticulina gottingensis/ Reinholdella*

This indicates, as is to be expected, that the different species occupy different habitats, indirectly reflected in different depth ranges.

Johnson (1976) has made a comprehensive attempt to evaluate the autecology of the Foraminifera species in the Middle and Upper Lias of Mochras. An appraisal of the environmental implications of the sediments and total biota is combined with statistical study of the diversity, equitability and wall structure ratios of the foraminiferal fauna. Diversity and equitability are measured according to the methods of Beerbower and Jordan (1969), who favour the use of the information function for measuring diversity. This formula measures the number of species and proportions without making assumptions about the underlying basis of the distributions. Maximum diversity is when species have equal frequency. The equitability ratio gives a value of 1 when the species are equally distributed (reach equal numbers in the same sample). Figure 9.3 shows the samples plotted against the diversity and equitability of the contained foraminiferal faunas. The samples have also then been grouped according to possible environment of deposition. It is assumed that diversity is highest in open marine conditions and decreases in environments restricted by stagnation of bottom waters or proximity to land, with shallowing and changes in other factors such as salinity and turbulence. Low equitability is considered to indicate high environmental stress. A fall in the calcareous/agglutinated wall structure ratio is also considered to indicate restricted nearshore environment, but to indicate offshore stagnant environments when it remains high (due to abundance of *Reinholdella)* together with low diversity.

This analysis has enabled the depth ranges of the species to be worked out on the basis of their distribution through the samples. The results reveal that the fauna is essentially middle shelf with extension landwards into the outer, inner shelf and seawards to the inner, outer shelf. The Nodosariida constitute some 70 per cent of the total species (80 out of 116) recovered and also approximately 70 per cent of the total numbers of individuals. The ranges of 55 nodosariids, taken from Johnson's chart, are shown in figure 9.4. It will be seen that many species belonging to the same genus, and subspecies belonging to the same species, have different ranges. As emphasised by Johnson, this underlines the importance of using

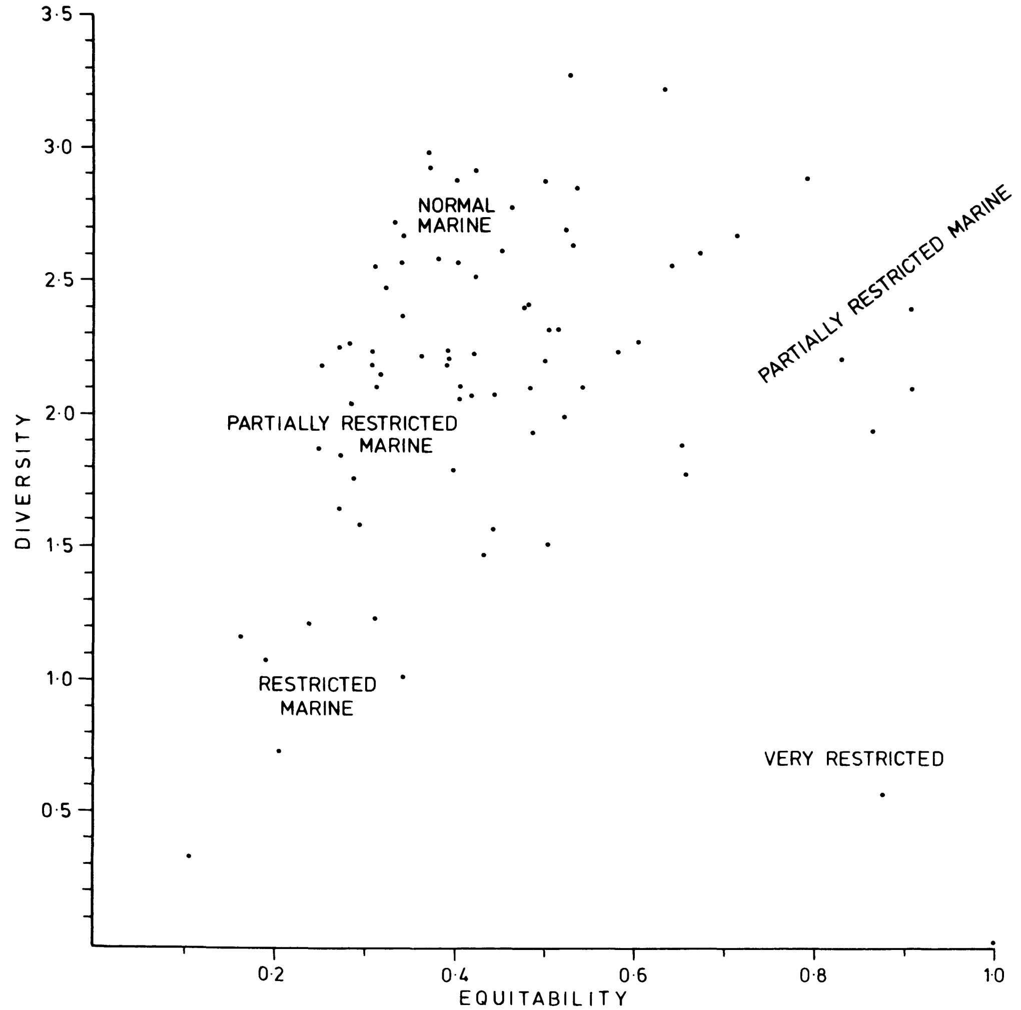


Figure 9.3 Samples from the Mochras Lias plotted against diversity and equitability and grouped according to possible environment of deposition. From Johnson (1976)

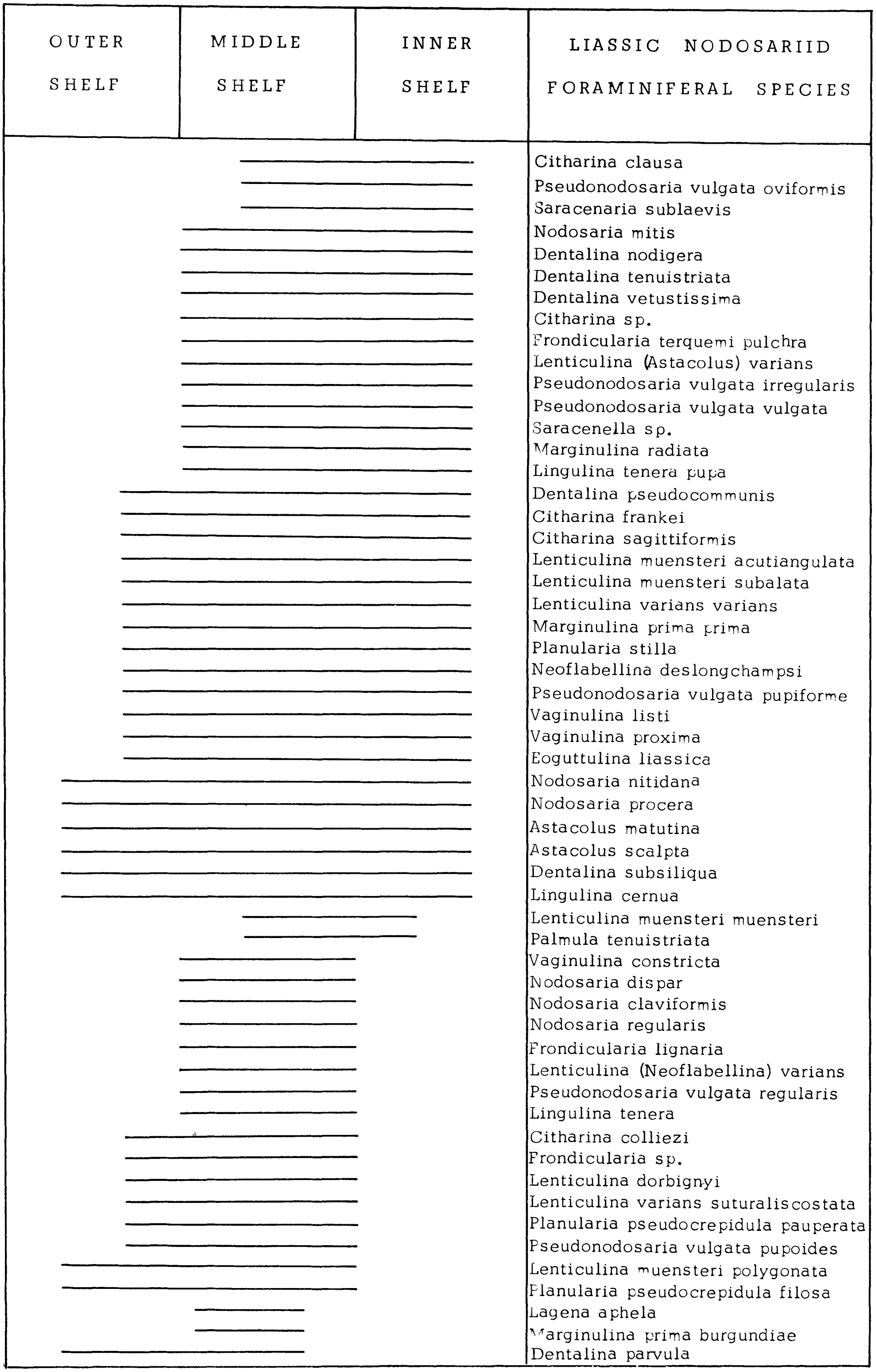


Figure 9.4 **Depth distribution of Upper and Middle Lias nodosariids from the Mochras borehole, N. Wales, showing concentration on the middle shelf with extension on to the outer and inner shelf. After Johnson (1976)**

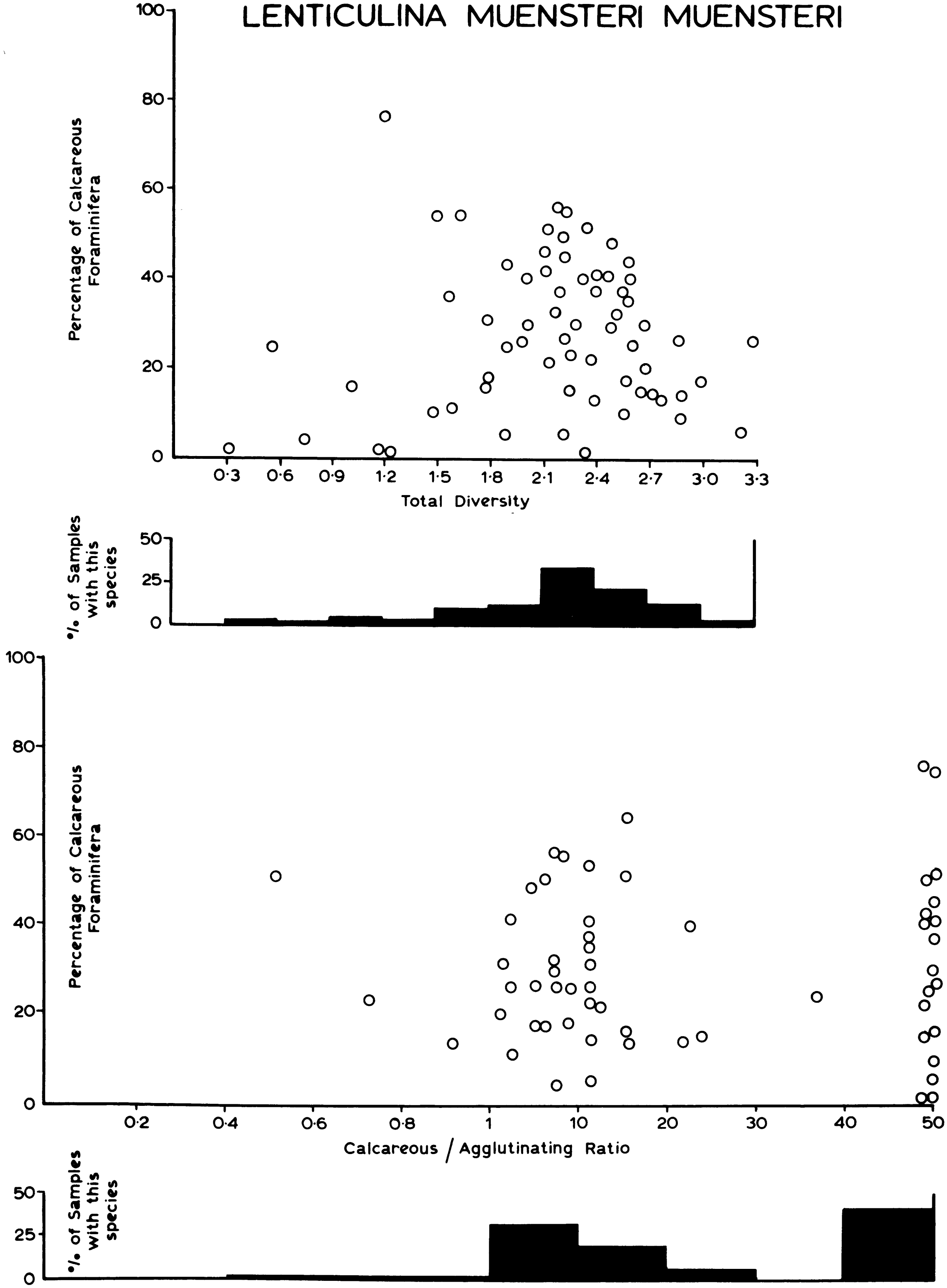
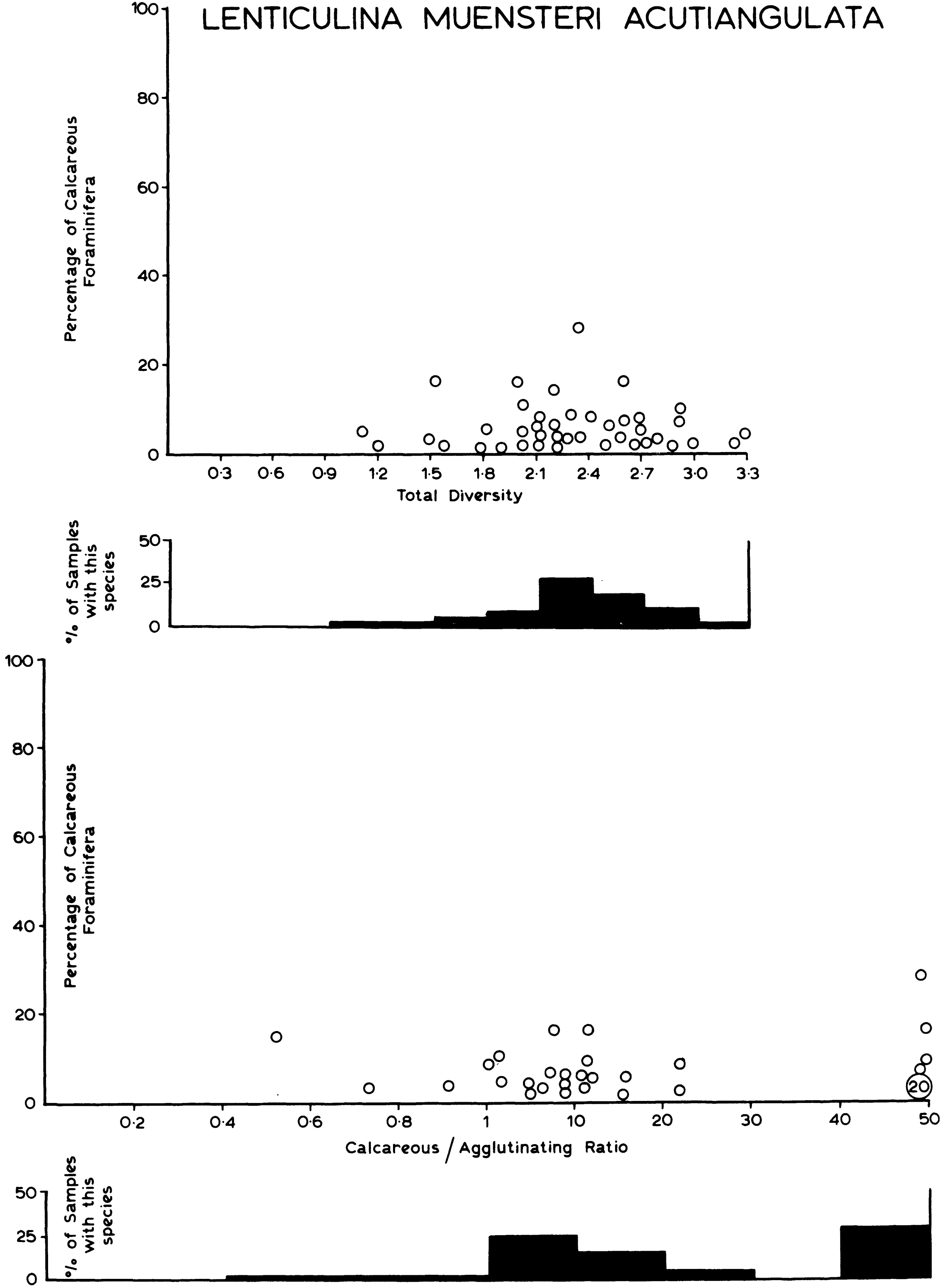


Figure 9.5 Samples with *Lenticulina muensteri muensteri* and *Lenticulina muensteri acutiangulata* plotted against



percentage of calcareous Foraminifera, diversity and calcareous/agglutinated ratio. From Johnson (1976)

taxa of this level of refinement in palaeo-ecology. In figure 9.5, samples with *L. muensteri muensteri* and *L. muensteri acutiangulata* are plotted against percentage of calcareous Foraminifera, diversity and calcareous/agglutinated ratio. *L. muensteri muensteri* shows the widest range, which is consistent with the idea that it represents the basic stock from which the other, more confined subspecies arose, more narrowly adapted to particular niches.

In the light of the suggestion made earlier that uncoiling trends represent adaptations to life near the sediment/water interface, it is interesting that an analysis of the nodosariids in Johnson's species list reveals: 13 per cent tight-coiled, 8 per cent partially uncoiled, 27 per cent uniserial flattened or palmate, 51 per cent uniserial round to oval, 1 per cent unilocular. This indicates a clear predominance of genera interpreted as infaunal and is consistent with a general midshelf habitat.

Copestake (1978) found that *Lenticulina ex gr. muensteri* and the *Lingulina tenera* plexus had a mutually exclusive relationship in the Lower Lias. This is explicable if *Lingulina,* like other flattened forms, was adapted to gliding over the surface of soft sediments, while *Lenticulina* was better adapted to firm substrates. The decline of *Lingulina* from the Middle Lias onwards may be due to competitive exclusion by *Frondicularia* with more advanced apertural coverplate system.

In sharp contrast to their position in the Jurassic, the Cretaceous retreat of the Nodosariida is well shown in the frequency diagram produced for the Albian by Price (1977). They are subordinate to other groups throughout but slowly increase to 25 per cent of the total in the Upper Albian. This increase coincides with a change from clay to marl, increasing temperature and maximum depth.

The move to deeper water appears to be connected not only with competition with other groups but with the great Cretaceous transgressions which brought slope depths to the outer shelves, and thus, ultimately, with Aptian – Albian rifting and the opening of the Atlantic (Sliter, 1972). That these conditions were favourable to the nodosariids is shown by the gradual increase in diversity through the Senonian into the Maastrichtian, already mentioned. An analysis of the lists (201 species) given by Krystyna Pozaryska (1957) shows that taken as a whole the Upper Cretaceous nodosariids in Poland are: close-coiled 10 per cent, partially uncoiled 12 per cent, uniserial flat or palmate 26 per cent, uniserial round to oval 30 per cent, unilocular 21 per cent. Uniserial forms predominate, as in the Lias, but there is only one species of *Lingulina.* In total contrast, unilocular genera reach 21 per cent. *Frondicularia* and *Palmula* are also strongly represented. However, the Nodosariida remained abundant in moderate, or even shallow, shelf depths until well into the Tertiary (Plummer, 1926; Haynes, 1958c; Larsen and Jørgensen, 1977), possibly indicating the influence of bottom conditions independent of depth.

This discussion should bring home to the student the difficulty of disentangling evolutionary events from environmental influences. Clearly, great care has to be taken in the interpretation of the relative frequencies of major groups if these are to be used in environmental reconstruction.

Returning to the problem of the origin of the Nodosariida, it is possible that the rise of the ancestral group of septate archaediscids was connected with the greater efficiency of the radial wall in symbiotic relationships. Also, as we have seen, the endothyraceans appear to have been restricted largely to the inner shelf (Mamet, 1977). Rapid, adaptive radiation of uncoiled nodosariids into deeper, midshelf environments may therefore explain their relatively high numbers in the Permian. The endothyraceans also appear to have been stenohaline, whereas *Lenticulina* was able to penetrate restricted environments, including brackish water, in the Mesozoic (Shipp, 1978). The replacement of the endothyraceans at the Permo-Triassic boundary may, therefore, be a direct consequence of the creation of the late Permian brackish ocean, due to abstraction of salt (Stevens, 1977), this being combined with the precipitous drop in phytoplankton levels claimed by Tappan and Loeblich (1973a) which caused the extinction of most suspension feeders and all but the most efficient grazers, carnivores and detritus feeders. Nearly half the total foraminiferal genera became extinct. The Nodosariida were also much reduced but the ancestral, *Lenticulina* stock survived the crisis to give a second, major wave of adaptive radiation in the Triassic.

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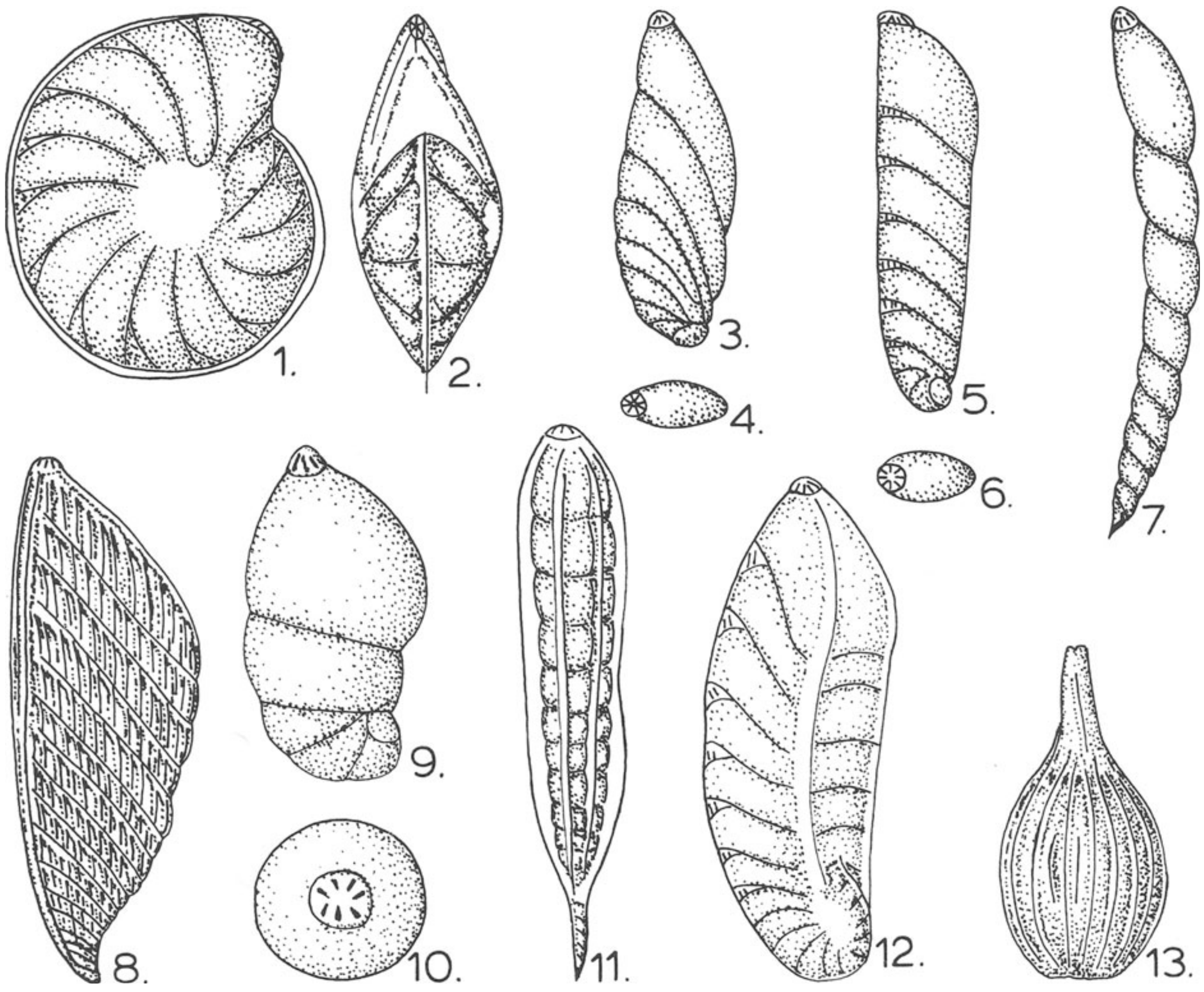
SUMMARY CLASSIFICATION

MAIN FAMILIES AND IMPORTANT GENERA OF NODOSARIIDA

NODOSARIIDA	wall radial hyaline, monolamellar or multilamellar; U. Palaeoz. – Rec. Key figures 9.6 and 9.7.
NODOSARIACEA	planispiral to biserial, uniserial and unilocular; aperture characteristically round with marginal slits or a closed trematophore with radiating slits or pores produced into a tube, or a simple slit; Perm. – Rec. Key figure 9.6.
NODOSARIIDAE	planispiral to uniserial or unilocular; aperture peripheral or terminal, usually radiate or with full trematophore; Perm. – Rec.
Lenticulina (nos. 1/2)	involute planispiral, lenticular; aperture peripheral; Perm. – Rec. (apertural slits enlarged in plane of compression and extending into apertural face = sub. gen. *Robulus;* porous trematophore = *Cribrorobulina,* Mio. – Rec.; adult mainly uncoiled—at least in A form—with last chambers not reaching the centre of coiling = sub. gen. *Astacolus* (nos. 3/4); same but very compressed = sub.gen. *Planularia;* same but triangular = sub. gen. *Saracenaria* (no. 12), Jur. – Rec.; astacoline with porous trematophore = *Cribrolenticulina* Haman 1978, Neo.).
Vaginulina (nos. 5/6)	uniserial, initial coil only in B form, with straight peripheral edge, compressed tabular or ovate section; aperture peripheral; Trias. – Rec. (triangular in section = *Saracenella* Franke 1936, Jur. – Rec.; coil in both generations = sub. gen. *Vaginulinopsis;* triangular also = *Tristix,* Jur. – Rec.; final chambers inverted V shape = *Flabellinella* (no. 14), Cret.).
Dentalina (no. 7)	elongate uniserial with recurved peripheral edge; ovate in section; sutures oblique to axis; aperture peripheral; Perm. – Rec.
Citharina (no. 8)	uniserial, initial part may be planularian or vaginuline, with later chambers becoming increasingly wide, producing a flattened, sub-triangular test; aperture peripheral; Jur. – Rec.
Marginulina (nos. 9/10)	uniserial, initial coil only in B form, inflated and round in section with terminal or peripheral aperture; Trias. – Rec. (fully planispiral initial part in both generations = sub. gen. *Marginulinopsis;* produced neck with rings = *Amphicoryna,* Neo. – Rec.).
Nodosaria (no. 11)	elongate uniserial, inflated and round in section; usually straight with sutures at right angles to axis (except in early part of B form); aperture terminal; Perm. – Rec. (chambers strongly embracing = *Pseudonodosaria;* oval pores in trematophore = *Chrysalognium,* U. Cret. – Rec.).
Palmula (no. 15)	planispiral lenticular to uniserial palmate in adult with inverted V-shaped chambers; aperture terminal; Jur. – Rec. (margin truncate and inverted chambers tending to reach back to base = sub. gen. *Neoflabellina,* U. Cret. – Pal.).

Frondicularia (no. 16)	uniserial elongate or palmate with inverted V-shaped chambers throughout at least in A form; compressed; aperture terminal, may be produced; Perm. – Rec. (narrowly elongate, chambers not reaching back to base = sub. gen. *Ichthyolaria,* Perm. – Jur.).
Lagena s.l.(no. 13)	unilocular; aperture produced with phialine lip and may be grooved, fluted or smooth (usually broken); Jur. – Rec.
LINGULINIDAE (*nom. transl.* Grigelis 1977)	planispiral to uniserial; aperture peripheral to terminal, elongate slit or oval; Perm. – Rec.
Ellipsocristellaria (nos. 21/22)	planispiral lenticular; aperture peripheral; L. Cret. (adult part uncoiled, compressed with terminal slit = *Lingulinopsis* (nos. 23/24), Cret. – Rec.).
Lingulina (nos. 25/26)	compressed uniserial throughout, chambers slightly inverted and considerably embracing, aperture terminal; Perm. – Rec. (elongate with less embracing chambers = *Lingulonodosaria,* Perm. – Cret.; round in section = *Gonatosphaera,* Tert.).
Rimulina (nos. 27/28)	unilocular, elongate oval and compressed aperture extending halfway down one side; Rec.
PLECTOFRONDICULARIIDAE (*nom. transl.* Montanaro Gallitelli)	biserial to uniserial, aperture terminal with trematophore; Cret. – Rec.
Lankesterina (no. 17)	flattened biserial throughout, periphery truncate; Olig.
Plectofrondicularia (nos. 18/19)	biserial to uniserial, inverted V-shaped chambers in adult, narrowly elongate; aperture with elevated margin; Eoc. – Rec. (uniserial throughout in A form = *Amphimorphina).*
Kyphopyxa (no. 20)	biserial to inverted V-shaped chambers in adult, palmate with chambers tending to reach back to base; initial part vaginuline in B form; Cret. (inverted V-shaped to biserial = *Dyofrondicularia,* Plio.).
POLYMORPHINACEA (n. superfam. herein)	chambers in a spiral, sigmoidal or biserial alternating series about a longitudinal axis, to uniserial and unilocular; aperture terminal with trematophore; Trias. – Rec. Key figure 9.7.
POLYMORPHINIDAE	spiral, with chambers less than 90° apart to quinqueloculine, in planes 144° apart, to uniserial; aperture terminal, without internal tube; Trias. – Rec.
Eoguttulina (no. 1)	chambers in an elongate spiral less than 90° apart, inflated, each set farther from the base; Trias. – L. Cret. (final chambers biserial = *Glandulopleurostomella,* Jur. – Olig.; biserial throughout = *Pyrulinoides* (nos. 2/3), Trias. – U. Cret.).
Sagoplecta (no. 4)	biserial to uniserial, later chambers angled, becoming inverted with retral processes; Trias.
Guttulina (nos. 5/6)	quinqueloculine and strongly overlapping, final chambers only slightly removed from base; Trias. – Rec. (quadriloculine = *Spirofrondicularia,* Jur. – L. Cret.).
Globulina (nos. 7/8)	quinqueloculine to triloculine, inflated chambers strongly overlapping; Jur. – Rec.
Pyrulina (no. 9)	triloculine to biserial, inflated, chambers strongly overlapping; Jur. – Rec.

Pseudopolymorphina (no. 10)	quinqueloculine to biserial without much overlap; Jur. – Rec. (biserial throughout, at least in A form, and flattened = *Polymorphina* (no. 11), Tert.).
Sigmomorphina (no. 12)	biserial with chambers added at slightly less than 180° and sigmoid gradually removed from base; Jur. – Rec. (later chambers reaching back to the base = *Sigmoidella* (no. 13), Cen.).
GLANDULINIDAE	triserial to uniserial and unilocular; aperture with internal tube; Cret. – Rec.
Dainita (nos. 14/15)	triserial to biserial, embracing; internal tube attached to one wall; Cret. (triserial throughout = *Siphoglobulina,* Cen.; same with short tube *Globulotuba* (nos. 16/17), Rec.).
Barnardina n. gen. herein (nos.18 – 20)	type *B. thanetana* n.sp. *Glandulina ? laevigata* and *G. ? ovula* Haynes (not d'Orbigny) 1958b, p.14, triserial to uniserial, strongly overlapping, uniserial throughout in A form, aperture with short internal tube; Tert.
Laryngosigma (nos. 25/26))	biserial sigmoid, overlapping; short internal tube; Rec. (plane biserial = *Esosyrinx* (nos. 21/22), Rec.).
Glandulina (nos. 23/24)	biserial to uniserial, globose and embracing, uniserial throughout in A form; short internal tube; Rec.
Oolina (no. 27)	unilocular, globose; short internal tube; Cret. – Rec.
FORM GENERA	possible growth stages resembling 'fistulose growth' (no. 31).
Bullopora (no. 30)	attached series of hemispherical chambers joined by stolon-like necks; aperture produced; Jur. – Rec. (chambers irregularly overlapping = *Sporadogenerina,* Rec.).
Ramulina (no. 32)	free series of globular chambers joined by stolon-like necks, apertures multiple, produced; Jur. – Rec.
'Webbinella' (nos. 28/29)	attachment form produced by different polymorphinids in which the test develops an encrusting flange and may lose its chambers by resorption; Cret. – Rec.

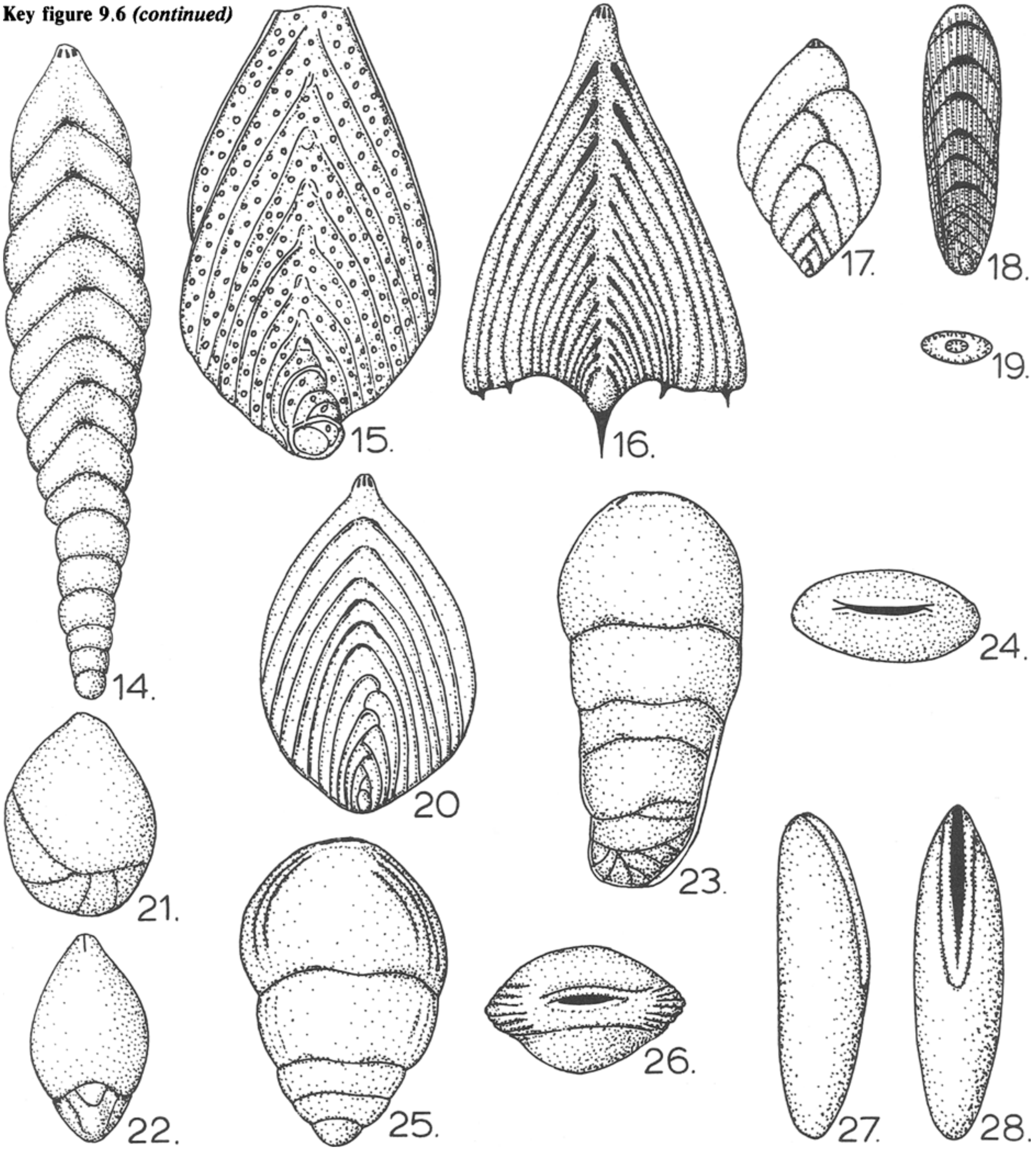


Key figure 9.6 Nodosariacea

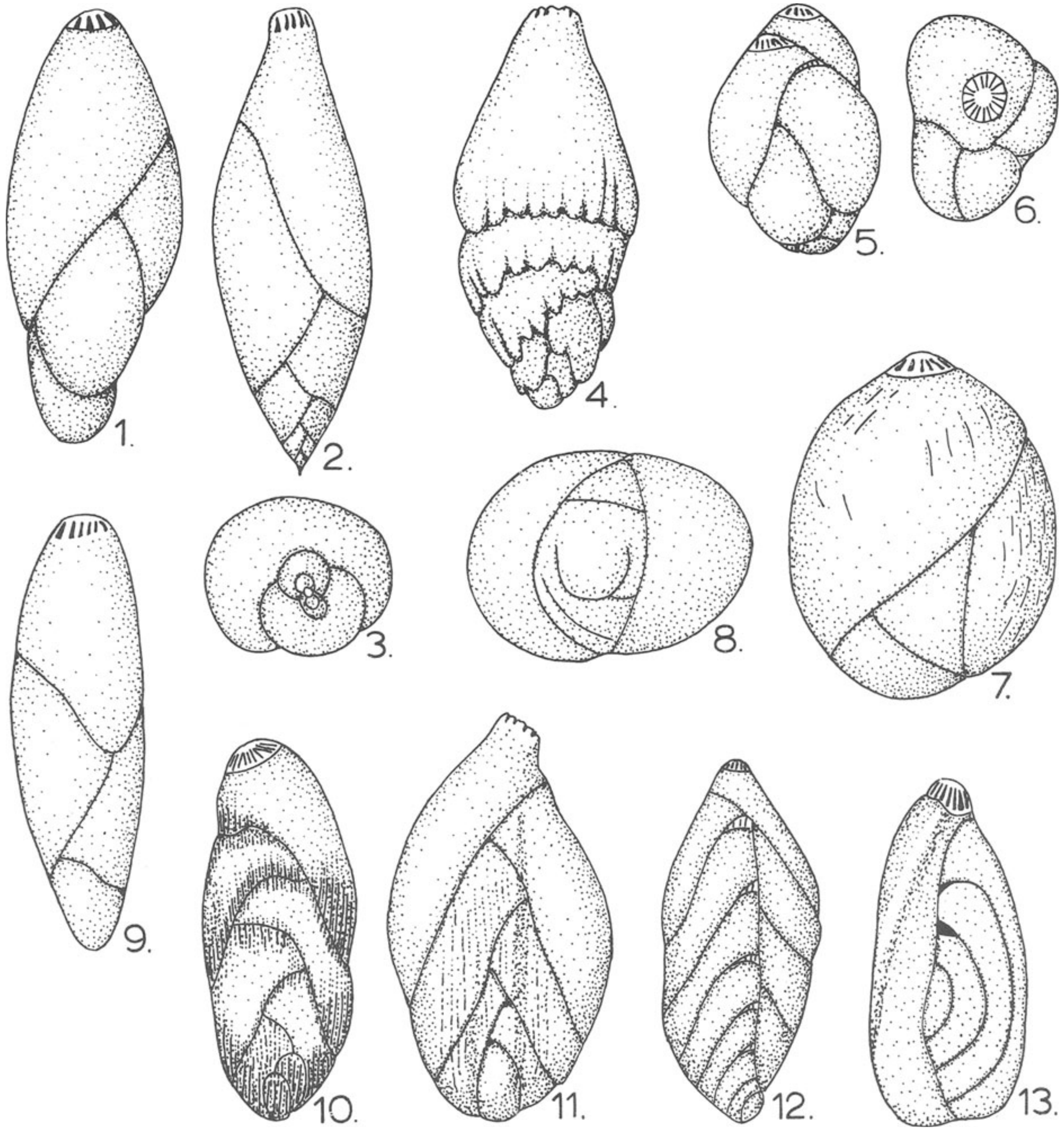
1/2 ***Lenticulina (Robulus) thalmanni*** **(Hessland), after Brady, × 12**
3/4 ***Astacolus insolitus*** **(Schwager), after Brady, × 60**
5/6 ***Vaginulinopsis sublegumen*** **(Parr), after Brady, × 30**
7 ***Dentalina bradyensis*** **(Dervieux), after Brady, × 15**
8 ***Citharina colliezi*** **(Terquem), after L. & T., × 48**
9/10 ***Marginulina obesa*** **(Cushman), after Brady, × 30**
11 ***Nodosaria lamnulifera*** **Boomgart, after Brady, × 15**
12 ***Saracenaria italica*** **Defrance, after Brady, × 20**
13 ***Lagena sulcata*** **(W. & J.), after Haynes, × 100**

(continued overleaf)

Key figure 9.6 *(continued)*



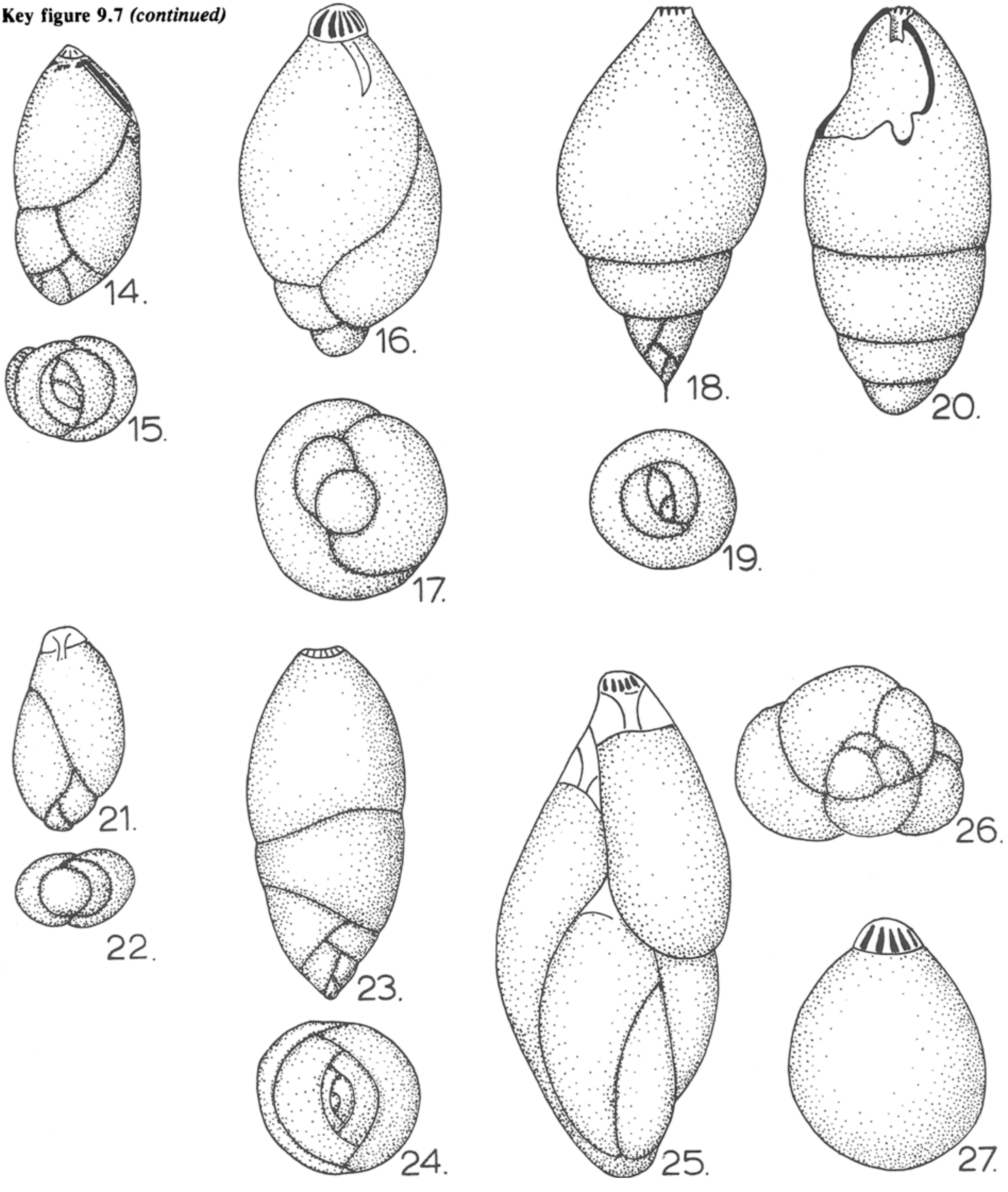
14 *Flabellinella zittelliana* **(Egger), × 25**
15 *Palmula (Neoflabellina) rugosa* **d'Orbigny, after L. & T., × 50**
16 *Frondicularia sagittula* **van den Broeck, after Brady, × 15**
17 *Lankesterina frondea* **(Cushman), after L. & T., × 80**
18/19 *Plectofrondicularia japonica* **(Asano), after L. & T., × 48**
20 *Kyphopyxa christneri* **(Carsey), after L. & T., × 28**
21/22 *Ellipsocristellaria sequana* **(Berthelin), × 80**
23/24 *Lingulinopsis carlofortensis* **Bornemann, after L. & T., × 20**
25/26 *Lingulina seminuda* **(Hantken), after Brady, × 12**
27/28 *Rimulina glabra* **d'Orbigny, × 50**



Key figure 9.7 Polymorphinacea
1 *Eoguttulina anglica* Cushman & Ozawa, after L. & T., × 150
2/3 *Pyrulinoides acuminatus* (d'Orbigny), after Barnard, × 180
4 *Sagoplecta goniata* Tappan, × 95
5/6 *Guttulina problema* d'Orbigny, after Brady, × 40
7/8 *Globulina* cf. *inaequalis* Reuss, after Haynes, × 100
9 *Pyrulina cylindroides* (Roemer), after Barnard, × 90
10 *Pseudopolymorphina ligua* (Roemer), after Brady, × 18
11 *Polymorphina anceps* Philippi, after Haynes, × 30
12 *Sigmomorphina pseudoregularis* Cushman & Thomas, × 25
13 *Sigmoidella kagaensis* Cushman and Ozawa, after L. & T., × 50

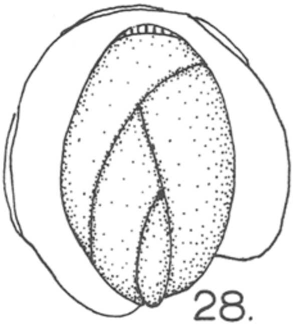
(continued overleaf)

Key figure 9.7 ***(continued)***



14/15 *Dainita siberica* **(Dain), × 47**
16/17 *Globulotuba entolsoleniformis* **Collins, × 150**
18–20 *Barnardina thanetana* **Haynes, × 100; 18/19 B form, 20 A form**
21/22 *Esosyrinx* **sp. Haynes, × 100**
23/24 *Glandulina laevigata* **d'Orbigny, after L. & T., × 50**
25/26 *Laryngosigma harrisi* **Haynes, × 100**
27 *Oolina laevigata* **d'Orbigny, after Haynes, × 170**

Key figure 9.7 ***(continued)***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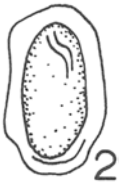
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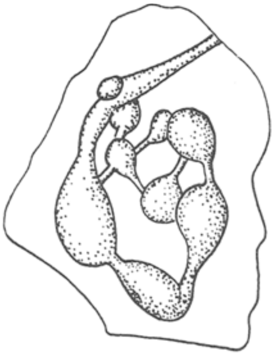
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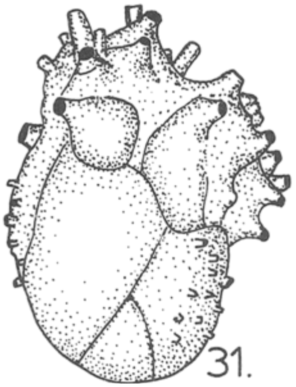
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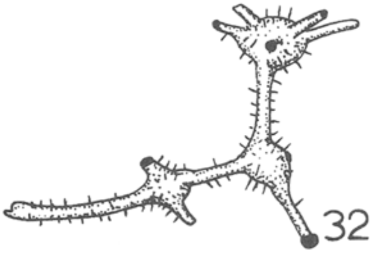
32.

28/29 ***Laryngosigma lactea*** **(W. & J.), after Haynes, × 100, =** ***Webbinella hemisphaerica*** **(Jones, Parker & Brady); 28 with attachment flange, 29 small specimen with chambers resorbed**
30 ***Bullopora rostrata*** **Quenstedt, after L. & T., × 20**
31 ***Globulina lacrima*** **Reuss, fistulose variety, after Barnard, × 90**
32 ***Ramulina globulifera*** **Brady, × 35**

Chapter 10

The Buliminida

> A study of foraminiferal assemblages of modern seas has disclosed striking correlations between form, structure and environment.... Among species of *Bolivina, Bulimina* and *Uvigerina,* small, less ornamented types occur on the continental shelf and there is a progressive increase and differentiation of surface sculpture with increasing depth of water.
>
> (Bandy, 1960)*

The Buliminida include some of the most beautiful glassy Foraminifera—elongate spirals or columns of bubble-like chambers with comma-shaped or delicately siphonate apertures and compressed blades with barbed carinae. They are densely perforated and the pores, often of different sizes and shapes, may be arranged in different patterns. The external surface is often variously ornamented with costae, nodes or spines which appear to afford a peculiar adaptive advantage in the fine sediments of the deep ocean floor.

A characteristic feature is the toothplate connecting the aperture with the previous foramen. This varies from a simple trough-like or cornet-shaped structure to a rolled-up tube, and may protrude through the aperture like a cockscomb (figure 10.1). It has been investigated in detail under the optical microscope by Höglund (1947) and Hofker (1951, 1956) and illustrated by SEM (Glaçon and Sigal, 1974). Although Hofker stresses the value of the toothplate as a key to phylogenetic relationships in the group, it is still not clear what taxonomic weight can be put on these differences and further work by SEM is required.

The wall is calcitic and both hyaline radial and hyaline oblique structures occur. An attempt was made in the 'Treatise' to subdivide the group on the basis of these differences in wall structure with all the oblique genera removed to the Cassidulinacea. This move has broken down because variation occurs at the generic and the specific level. It was indicated by the results of Wood (1949a), who found that although *Ehrenbergina serra* sensu Brady is hyaline oblique, *E. hystrix* is radial. *E. hystrix* var. *glabra,* however, is consistently hyaline oblique. He also discovered that *Pleurostomella subnodosa* sensu Brady is compound with an oblique inner layer and an outer pellicle of radially disposed crystals. These variations have been confirmed both in the Cassidulinidae (Feyling-Hanssen and Buzas, 1976) and in the Turrilinidae (Hansen, 1972).

As pointed out earlier (chapter 4), the wall in all the hyaline Foraminifera apart from the Nodosariida is regarded as fundamentally bilamellar. Sliter (1974), after a study of the ultrastructure of members of the Bolivinitidae and *Caucasina,* regarded them as 'essentially monolamellar' but with a surface veneer. He distinguished the following layers: a spongy organic lining, basal membrane, calcitic wall, calcitic veneer and outer membrane. Two calcitic lamellae are therefore present in the wall of each new chamber, as in strictly bilamellar forms. The pores are simple 'protopores' and lack sieve plates.

CHAMBER FORM AND COILING MODES

As is well shown by the table of coiling modes (figure 4.3), almost 100 genera were placed in this order in the 'Treatise' (Loeblich and Tappan, 1964) and high trochoid arrangement is clearly dominant, reaching 70 per cent. Significantly, a similar high proportion is achieved only in the Lituolida. Biserial to uniserial arrangement reaches 17 per cent and enrolled biserial 10 per cent. Low trochoid and fully uniserial genera (in both generations) are rare, two only in each case. No unilocular forms were included in this group in the 'Treatise' but *Parafissurina,* and certain species placed in *Lagena,* probably belong here.

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*See Bandy (1960a).

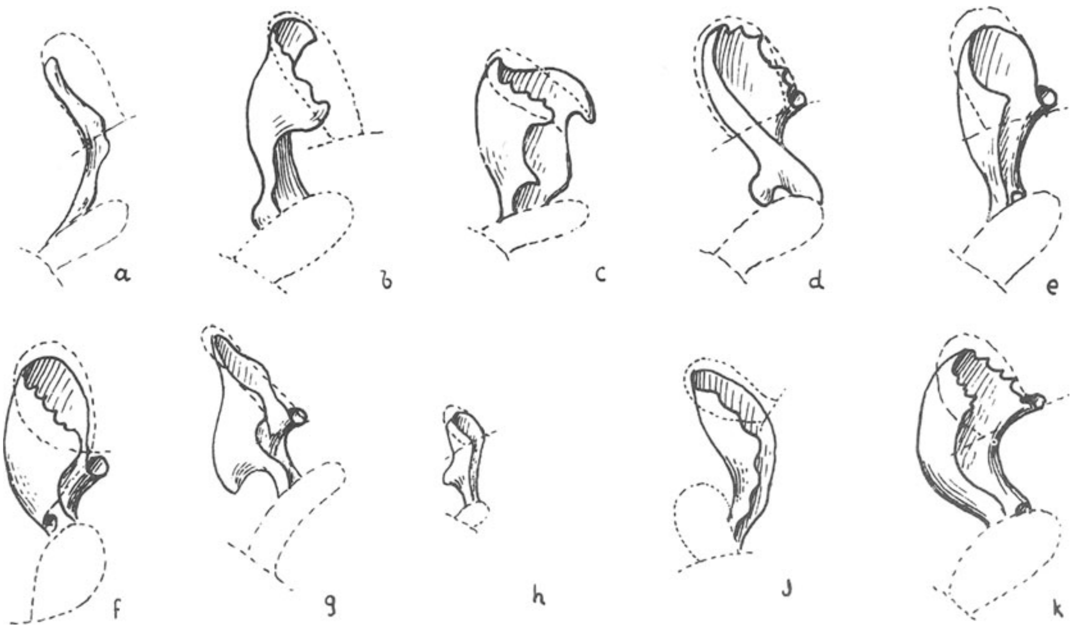

Figure 10.1 Toothplates in the Buliminidae. a *Praebulimina* sp., b *Bulimina trigonalis,* c *Bulimina rostrata,* d *Bulimina inflata,* e *Bulimina buchiana,* f *Bulimina marginata,* g *Reusella spinulosa,* h *Chrysalidinella,* j *Bulimina debelis,* k *Bulimina aculeata.* From Hofker (1951)

There are no attached forms and as in the case of the Nodosariida there are no examples of secondary subdivision of the chambers, although retral processes occur rarely.

The superfamilies and families are distinguished on the basis of chamber arrangement and aperture form. See the Summary Classification at the end of the chapter.

Buliminacea

Trochospiral to triserial, biserial and uniserial genera, usually round or trigonal in section with globular chambers and umbilical, basal to comma-shaped aperture, are included in the Buliminacea. The aperture becomes terminal and round in advanced forms and finally produced with a turned out (everted or phialine) lip. The toothplate is trough-like or cornet shaped with free edge produced and wing-like or rolled up to form a tube.

Trochospiral genera with more than three chambers to the whorl, at least in the initial part, are included in the Turrilinidae. Triserial to uniserial genera with comma-shaped or terminal aperture are included in the Buliminidae. This family includes species with oval to slit-like pores, sometimes of two sizes in the same individual and in advanced forms the free edge of the toothplate is rolled up and joins the anterior end of the aperture. Triserial to uniserial genera with produced aperture, characteristically with a long neck and phialine lip, are included in the Uvigerinidae. Triserial to uniserial genera with triangular or arched chambers and basal to cribrate apertures are included in the Pavoninidae.

The toothplate shows considerable variation in this superfamily, as revealed by the optical microscopic researches of Höglund (1947), Hofker (1951), Haynes (1954), Nørvang (1966, 1968a, 1968b), and SEM (Glaçon and Sigal, 1974; Scott, 1977). Hofker distinguished a number of genera largely upon the basis of this feature, as for instance *Euuvigerina* which has a trough-like toothplate lacking the wing-like free edge of *Uvigerina.* However, there are similar differences between Palaeocene species still referred to *Bulimina,* such as *B. thanetensis* and the genoholotype *B. marginata* which has a rolled-up free edge. Before these differences are accepted as generic or even subgeneric further genera, especially *Neobulimina,* and a broad range of species must be examined. For the same reasons the Turrilinidae are distinguished from the Buliminidae here on the basis of their trochospiral arrangement rather than their supposed simpler toothplate, as in the 'Treatise'. This is because this structure has not been described in *Turrilina,* although the SEM photos of Hansen (1972) appear to show a cornet-shaped toothplate with denticulate free edge, possibly not unlike that of *Stainforthia*. *Caucasina,* although hyaline oblique, is included here in the Turrilinidae, as is *Epistominella* which appears close to *Baggatella* despite its peripheral, rather than umbilical, aperture.

The Buliminidae like the Turrilinidae are regarded as including both hyaline radial and oblique genera and species. For this reason *Fursenkoina* and *Cassidella* are placed close to *Stainforthia.*

Bolivinitacea

Compressed biserial to uniserial genera and enrolled biserial to uncoiled forms with aperture in the plane of compression, umbilical to terminal, are included in the superfamily Bolivinitacea.

The family Bolivinitidae includes the biserial to uniserial genera with aperture extending into the apertural face from the basal suture or becoming terminal or rounded. The Eouvigerinidae exhibit similar chamber arrangement but the aperture is terminal with a produced neck and lip. In contrast, the Islandiellidae are enrolled biserial to uncoiled with basal to subterminal aperture.

Most, if not all, of the genera in the Bolivinitidae appear to be hyaline radial, if we continue to exclude *Loxostomum,* following Loeblich and Tappan (1964). This can be justified on the grounds of complete absence of a toothplate in this genus, which is consistently present in other members of the superfamily. Indeed, Copestake (1978) suggests that the hyaline oblique *Loxostomum* gave rise to radial *Berthelinella* in the Lias. The Loxostomidae clearly require further study.

Although the Islandiellidae were originally distinguished as hyaline radial in wall structure, populations of *Islandiella islandica* from Rockall Trough and the North Sea are consistently hyaline oblique (specimens from G. Pearce and D. Masson collections, U.C.W.), although identical in other external and internal characters with the populations from Iceland originally studied by Nørvang (1958). If these populations can interbreed this represents variation in wall structure at the infraspecific level, as noted above in *Ehrenbergina.* Variation in wall structure at the specific level has also been confirmed in *Cassidulina* by Feyling-Hanssen and Buzas (1976). This has led these last authors to regroup *Islandiella* with *Cassidulina.* This course is not followed here because the Islandiellidae can be clearly differentiated upon the basis of the consistent presence of a cornet-like toothplate, connecting the aperture with the previous foramen.

Cassidulinacea

This superfamily includes triserial to biserial and uniserial genera and enrolled biserial to uncoiled forms with subterminal to terminal or peripheral aperture. The lower margin of the aperture is characteristically dentate and there is an internal tube or siphon, although this may be lost or reduced in advanced forms. The Pleurostomellidae include the triserial to biserial and uniserial genera, usually with globular and embracing chambers and crescentic aperture with dentate lower border and internal siphon. The siphon is much reduced in *Ellipsolingulina.* In the Cassidulinidae the toothplate is reduced to a short blade projecting internally from the inner border of the aperture and the chamber arrangement is enrolled biserial. In the streptospiral *Sphaeroidina* the toothplate is lost altogether but an external tooth is retained on the lower or outer border of the aperture, as in *Cassidulina.*

Most genera in the Pleurostomellidae are hyaline oblique but the unilocular *Parafissurina* is hyaline radial. For this reason it was transferred to the Glandulinidae in the 'Treatise'. However, the subterminal aperture beneath a hood and the long internal siphon indicate that an affinity with the Pleurostomellidae is more likely. *Sphaeroidina* was placed in a separate family in the 'Treatise', within the Buliminacea which were considered a radial group. It is here considered an advanced member of the Cassidulinidae, following Vašíček (1956). As noted above, a number of radial species of *Cassidulina* are now known, including *C. cushmani* and *C. delicata,* so a major objection to this course disappears.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

There are only doubtful records of the order in the Triassic, but both the Buliminacea and the Bolivinitacea are apparently present in the Jurassic. The Cassidulinacea arose in the Cretaceous and most families had appeared by the end of the period except the Pavoninidae, the Islandiellidae and the Cassidulinidae. All families show continued diversification with evolution of new genera through the Cenozoic.

Both Cushman (1948) and Glaessner (1945, see reprint 1963a) considered that the buliminaceans were the most primitive group and probably arose from *Turrilina* and gave rise later to the bolivinitaceans and cassidulinaceans. Hofker (1951) in contrast, in the introductory part of his Siboga Report, considered the possibility that all three groups may have arisen separately from the agglutinating Valvulinidae. But later on he concluded that both the Buliminidae and Turrilinidae (Buliminellidae) arose separately from *Praebulimina.* He further proposed that the Bolivinitidae sprang from *Fursenkoina (Virgulina),* while *Cassidella* gave rise separately to the Cassidulinidae and the Pleurostomellidae. Loeblich and Tappan (1974) consider the possibility that *Deckerellina* (Palaeotextulariidae) was ancestral to the Buliminacea.

Pertinent to this discussion is the position of *Brizalina liassica* which is widespread in the Lower Jurassic. According to Nørvang (1957) and Witthuhn (1968) this species is aragonitic. *Neobulimina* has now been discovered in the Lias also (Copestake, 1978). The preservation of *Neobulimina bangae* and *B. liassica* in the Mochras Lias is identical. Copestake therefore suggests that both were aragonitic and that *N. bangae* gave rise to *Brizalina liassica* in the obtusum zone of the Sinemurian. This indicates to him that the Buliminida originated from the aragonitic Oberhauserellidae. On the other hand, the toothplate in these species is a broad, flat plate, different from the narrow trough-like toothplate in *Praebulimina.* Probably *'Neobulimina bangae'* and *Brizalina liassica'* represent a separate line of development in the aragonitic group and should be removed to the Robertinida (as here understood).

This leaves open the question of the origin of the Buliminida with *Praebulimina,* known from the Middle Jurassic, left as the most likely ancestral form. *Turrilina* is not known before the Eocene, so seems unlikely to represent a key, evolutionary link form. *Praebulimina* may have evolved from a triserial member of the Ataxophragmiidae with comma-shaped aperture and toothplate like *Eggerelloides* (see plate 7). *Eggerelloides* is not known before the late Cenozoic but the closely allied *Migros* is known from the Jurassic. The loosely spiral members of the Turrilinidae may have risen separately from a genus such as *Arenobulimina* and the low trochospiral genera appear to represent a distinct line of development within this group (subfamily Baggatellinae).

The Uvigerinidae probably also stem from *Praebulimina* but there may be two distinct lines: one leading from the Upper Cretaceous *Pseudouvigerina* to *Trifarina* in the Palaeocene and *Siphouvigerina* and *Siphogenerina* in the Eocene, and the other to *Uvigerinella* in the Palaeocene and *Uvigerina* in the Eocene. The ancestral genus in the Pavoninidae is *Reussella* which may have arisen directly from *Bulimina* in the Eocene.

The Eouvigerinidae arose from among the Bolivinitidae (probably *Brizalina)* in the early Cretaceous and completely uniserial forms, *Siphonodosaria* and *Stilostomella,* had evolved by the end of the Period. As pointed out by Glaessner, *Islandiella* is apparently an enrolled bolivinitid and appears to have arisen near the Mesozoic/Cenozoic boundary from *Brizalina.* The secondarily uncoiled forms *Cassidulinoides* and *Ehrenbergina* appear in the Eocene and the completely uncoiled *Orthoplecta* in the Quaternary.

Although *Pleurostomella* is reported from the Lower Cretaceous, the apparently more primitive, triserial to biserial *Wheelerella* and *Bandyella* occur in the early Upper Cretaceous. These genera may be nearer to the ancestral form. Although Hofker produced convincing evidence to show that the siphon in early chambers of *Pleurostomella* is narrowly open, as in *Cassidella,* this genus is not recorded before the Upper Cretaceous. The origin of the Pleurostomellidae therefore remains in doubt. But it seems quite likely that *Cassidulina* arose from a compressed, biserial pleurostomellid like *Wheelerella* in which the subterminal aperture became a slit parallel to the periphery and the siphon was reduced as in *Ellipsolingulina.*

All the families show a strong tendency to reduction in chamber number and appearance of uniserial growth. Unilocular genera apparently evolved in both the Uvigerinidae, *'Lagena'* with neck and phialine lip, and in the Pleurostomellidae, *Parafissurina.* This reduction in chamber number is generally accompanied by a change in the position of the aperture to terminal. However, it is noteworthy that in the Buliminidae, and especially in the Eouvigerinidae and Uvigerinidae, fully terminal apertures appear together with triserial and biserial chamber arrangement. Complication of the toothplate is seen particularly in the Buliminidae with rolled-up free edge in late Cenozoic *Bulimina* and double folding in *Globobulimina,* early in the Palaeogene.

Living individuals of the *Bulimina elongata* group occur with the apertural face adpressed to various firm substrates in Cardigan Bay, including mollusc shells (Haward and Haynes, 1976). The foraminifer clings by means of its pseudopods and ectoplasmic film, the test being held up at an angle of about 60°. The cylindrical form is relatively stable hydrodynamically (see figure 4.7) and can be orientated down-current. The initial spine probably acts as a protective device. Other genera with basal and comma-shaped aperture probably adopt similar life positions, and also those genera with enlarged, flattened and often triangular face. Thus *Bolivinita* may occur upright on firm substrates like *Textularia truncata* in Cardigan Bay and orientate itself to the current in a similar fashion. But there seems little doubt that hydrodynamically unstable, elongate and carinate, blade forms, including most species of *Bolivina* and *Brizalina,* are gliding forms lying flat on the bottom (as seen in the photographs of culture dishes of *Bolivina doniezi,* published by Sliter, 1970). Interestingly, many develop longitudinal ornament like *Lingulina* and *Frondicularia.*

The movement of the aperture to the terminal position and development of a neck is considered to represent an adaptation connected with feeding at or below the sediment/water interface (as discussed in chapter 4 and in relation to similar trends in the Agglutinating Group and the Nodosariida). This is well seen in the Uvigerinidae and in the Pleurostomellidae where embracing, globular chambers (hydrodynamically stable) are characteristic, as in the Glandulinidae. This shape would help partially buried forms to overcome the difficulty of orientating to changing currents. In fully infaunal genera an elongate cylindrical shape is probably more adaptive.

Compared with the Nodosariida, the number of completely uniserial genera is low. This could be explained as indicating low numbers of fully infaunal genera. It is more simply explained as reflecting the high proportion of elongate trochospiral forms which could be regarded as preadapted to an infaunal life. In the Nodosariida, uncoiled genera tend to be assymetric in shape until the initial coil is lost. It is noteworthy that among the bolivinitaceans the fully uniserial *Siphonodosaria* is the end product of a line of development from a blade form, the compressed biserial *Eouvigerina.* The complication of the evolutionary pathways followed by some families in this group is well illustrated by the reappearance of a close-coiled test form in the secondarily enrolled *Islandiella* and *Cassidulina,* presumably indicating a return to mobile surface feeding. But once again, by the Eocene, marked uncoiling trends supervene.

STRATIGRAPHICAL USE OF THE BULIMINIDA

The Buliminida became abundant by the Upper Cretaceous and are characteristic of Cenozoic assemblages, especially in sediments representing Outer Shelf and Slope depths (see further below). Several families do not appear until the Tertiary and the time of first occurrence of many genera is stratigraphically useful. There is a strongly marked influx of new forms in the Eocene and this group has found particular application in the biostratigraphical zonation of the Middle Tertiary as well as in the Upper Cretaceous.

A number of authors have attempted to achieve the refinements possible through close definition of the species in particular lineages. In the Upper Cretaceous most attention has been paid to the *Bolivinoides* group. Thus, Hiltermann and Koch (1950) found that the Senonian to Maastrichtian interval to N.W. Germany could be zoned on the series: *Bolivinoides strigillata — B. decorata decorata—B. miliaris—B. decorata delicatula—B. draco draco—B. decorata gigantea.* With modifications this scheme has now been applied worldwide: in Australia (Edgell, 1954), England (Barr, 1966), France (Hinte, 1967), Libya (Barr, 1970) and the USA (Petters, 1977). Several lines are now recognisable and Petters distinguishes a central stock leading from *B. strigillata* through *B. culverensis, B. decoratus* and *B. miliaris* to *B. draco* and side lines to *B. giganteus* (raised to specific rank) and through *B. praelaevigatus* to *B. laevigatus.* The close similarity in the ranges of the main elements in this plexus in England and Libya are well shown in figure 10.2.

Bolivinoides is useful only up to the Lower Maastrichtian and is replaced by other index benthonic species in the Upper Maastrichtian, but these include two species of *Pseudouvigerina* (Surlyk and Birkelund, 1977). The work on the Maastrichtian White Chalk by these authors is a good example of an integrated study of several faunal groups. As emphasised earlier, the student should note that although in this book we are dealing exclusively with Foraminifera their value is much increased when the results are combined with those of the study of other groups.

Uvigerina is a very useful genus in stratigraphy from the Eocene onwards and Vella (1961) distinguished several lineages in the Tertiary of New Zealand. The generalised scheme given by Hornibrook (1968) is reproduced in figure 10.3. Further work world wide has been carried out by Papp and Schmid (1971), Schmid (1972), Boersma and Berggren (1972), Lamb and Hickernell (1972), Daniels and Spiegler (1977) and Boersma (1977), and seven zones can be distinguished in the Miocene of N.W. Germany on the basis of the *U. semiornata* and *U. pygmaea* groups.

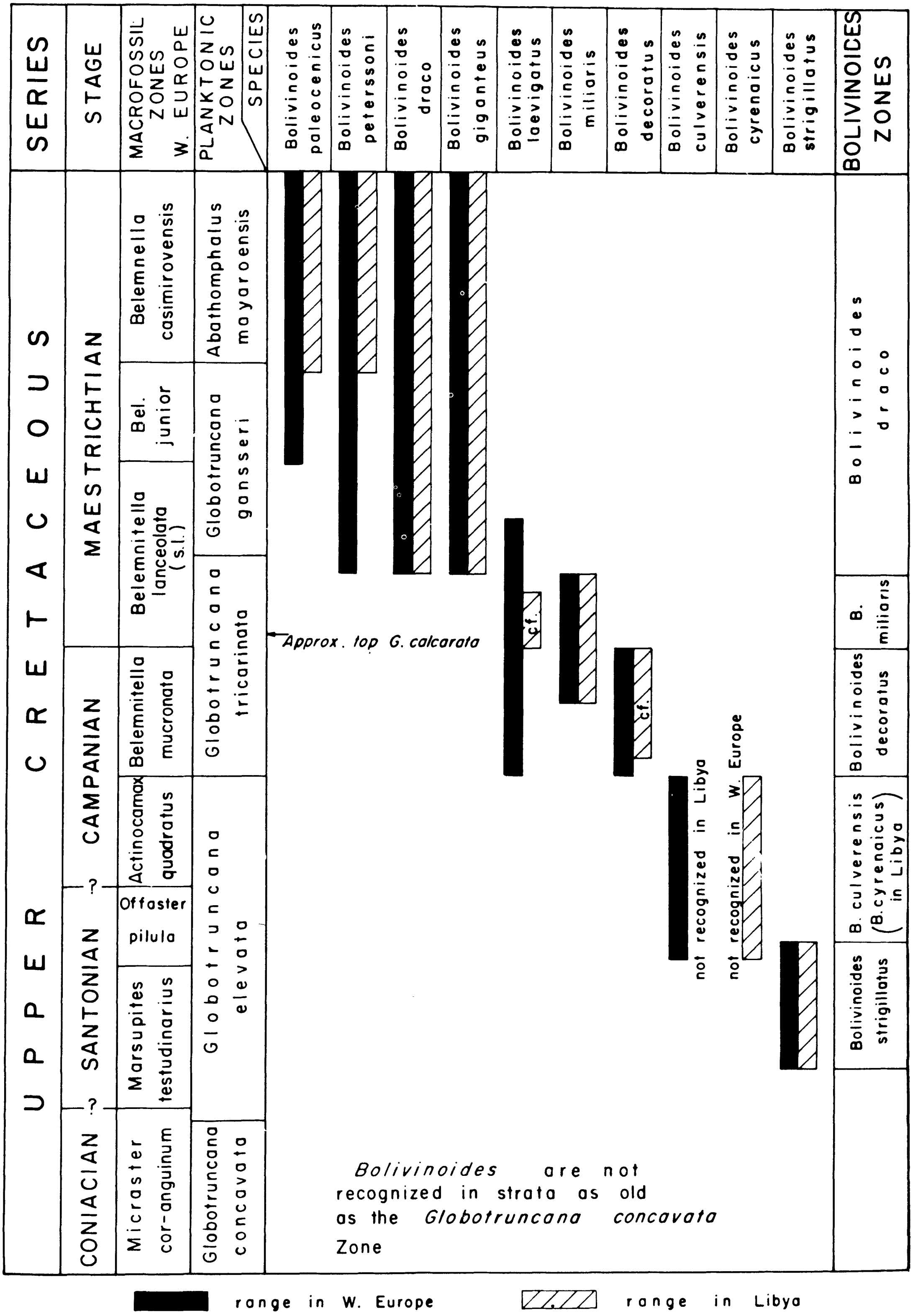

Figure 10.2 Comparison of the ranges of *Bolivinoides* species in N.W. Europe and the Tethyan Region. From Barr (1970)

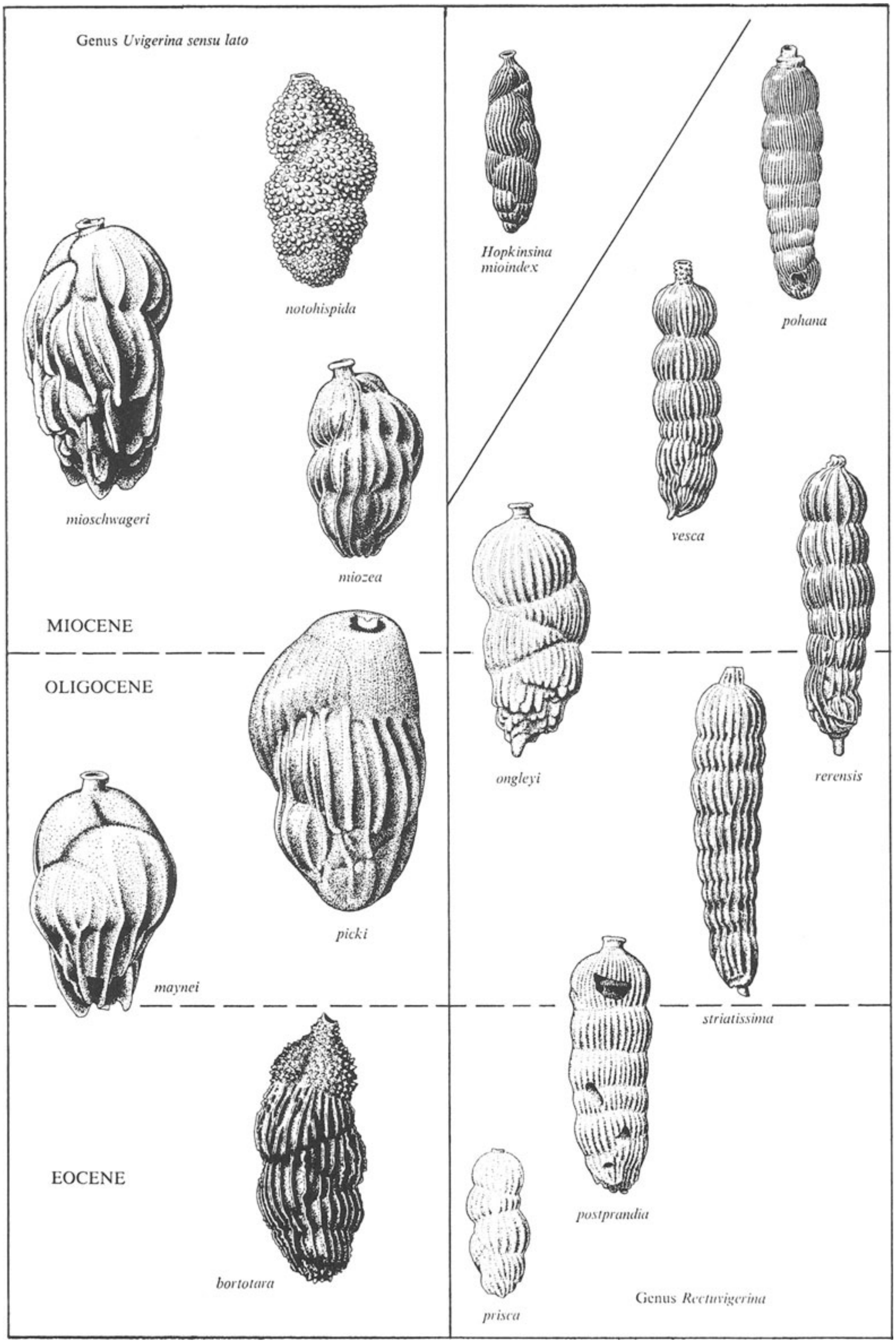

Figure 10.3 Sequence of uvigerinids in the New Zealand Tertiary. From Hornibrook (1968); illustrations by Brazier

According to Anne Boersma there are four time intervals with high numbers of new appearances of uvigerinids: Middle to late Eocene, early Oligocene, late Oligocene and early Miocene. She recognises three groups of species of *Uvigerina* on the basis of ornament—hispid, hispido-costate and costate—and regards them as an evolutionary series that first developed through the early Palaeogene but was repeated many times later in the Cenozoic. She also remarks on the cosmopolitan distribution of many species and their rapidity of dispersal around the world's oceans.

Evolutionary studies have also been made of *Ehrenbergina* and the results applied to Oligo-Miocene stratigraphy. Dorothee Spiegler (1973) has traced an evolutionary line from *E. variabilis variabilis* to *E. variabilis aculeata* in the Upper Oligocene and to *E. serrata serrata* and *E. serrata healyi* in the early Miocene in N.W. Germany. A parallel line is *E. variabilis variabilis* to *E. variabilis praepupa* and *E. pupa*. Both lines are considered to be examples of gradual change to more compact, solid forms. In New Zealand a parallel series has been used to define stage boundaries in the Lower Miocene. Formerly the base of the Otaian Stage was defined on the appearance of *E. healyi* which was considered to diverge to give *E. marwicki* and *E. willetti* in the Middle and Upper Otaian. Detailed measurements of the relation between length against gross inflation and length against width have been made by Scott (1973c). This work (figure 10.4) indicates that *E. healyi* and *E. marwicki* cannot be separated subspecifically and should both be referred to *E. marwicki*. *E. willetti* is considered a subspecies of *E. marwicki*. This has simplified treatment of this group and the species and subspecies can now be considered to jointly define the base of the Otaian.

ECOLOGY

The Buliminida occur widely from shallow, coastal waters to the Abyssal Plain but are particularly abundant on the Outer Shelf and on the uppermost Continental Slope (Norton, 1930; Parker, 1948; Lowman, 1949; Phleger, 1960; Murray, 1973b; Boltovskoy and Wright, 1976). For example, of 30 species found living at depths from 796 to 6011 m in the Peru – Chile Trench, 18 (60 per cent) belong to this order (Bandy and Rodolfo, 1964). The most common genera are *Bolivina, Brizalina, Bulimina, Cassidulina, Epistominella, Trifarina* and *Uvigerina*. These are also the most common forms on the Slope off Portugal (Seiler, 1975) and in the Bay of Biscay from 180 to 3000 m depth (Caralp *et al.*, 1970).

Epistominella is included in the list of genera that make up Brouwer's *'Cibicides wuellersdorfi* Fauna', characteristic of oceanic depths to 5000 m (1973). Strikingly, *Epistominella exigua* is the single most abundant species in Rockall Trough (Pearce, 1980).

Cassidulina, Trifarina and *Uvigerina* in particular can withstand subzero temperatures and are strong elements in temperate and high latitude faunas. *Uvigerina* is found down to the CCD and it is interesting that *Stilostomella antillea* is found live at 6011 m in the Peru – Chile Trench. This parallels the ability of certain shallow marine calcareous forams to penetrate low alkalinity environments where, after death, the abandoned tests are rapidly dissolved. *Cassidulina* is the most abundant genus in the Malin Sea (N.E. Atlantic). *C. laevigata* makes up more than 20 per cent of the total fauna and at the top of the Slope exceeds 30 000 individuals per 10 ml volume sample. *Cassidulina obtusa* also exceeds 5000 individuals per 10 ml (Pendlebury, 1974).

Cassidulina is very abundant nearshore in cold waters and occurs close to melting glaciers in Spitzbergen (Nagy, 1965). As might be expected, it has found particular application in palaeo-ecological interpretation in the Quaternary (Feyling-Hanssen *et al.*, 1971; Norris, 1972). *Uvigerina* has also been used as a cold-water indicator and Lutze (1978) in a study of JOIDES cores from between the Canaries and Africa finds that the *Uvigerina* maximum coincides with a Neogene cooling trend well shown by the planktonic Foraminifera. This genus appears to build its test in isotopic equilibrium with sea water (Shackleton, 1974) and variations in oxygen isotope ratios in Quaternary species can be related to climatic fluctuations (see chapter 14 for an extended treatment of oxygen isotope work on Foraminifera). In addition, variations in carbon-13 in *Uvigerina* through the late Pleistocene and Holocene can be related to a two-thirds reduction in tropical rainforests (which contain more than half the total carbon) at the height of the last glaciation, followed by their expansion to half as much again over their present area in the subsequent pluvial (Shackleton, 1977c). So remarkably, the test of a small, deep-water foram is found to faithfully monitor dramatic changes in the terrestrial, plant biosphere.

In part, the success of this group at great depths is related to their ability to tolerate lowered oxygen levels. This is indicated by a study of samples from the oxygen minimum zone of the Chilean Shelf (0.14 ml/l to 0.31 ml/l). They con-

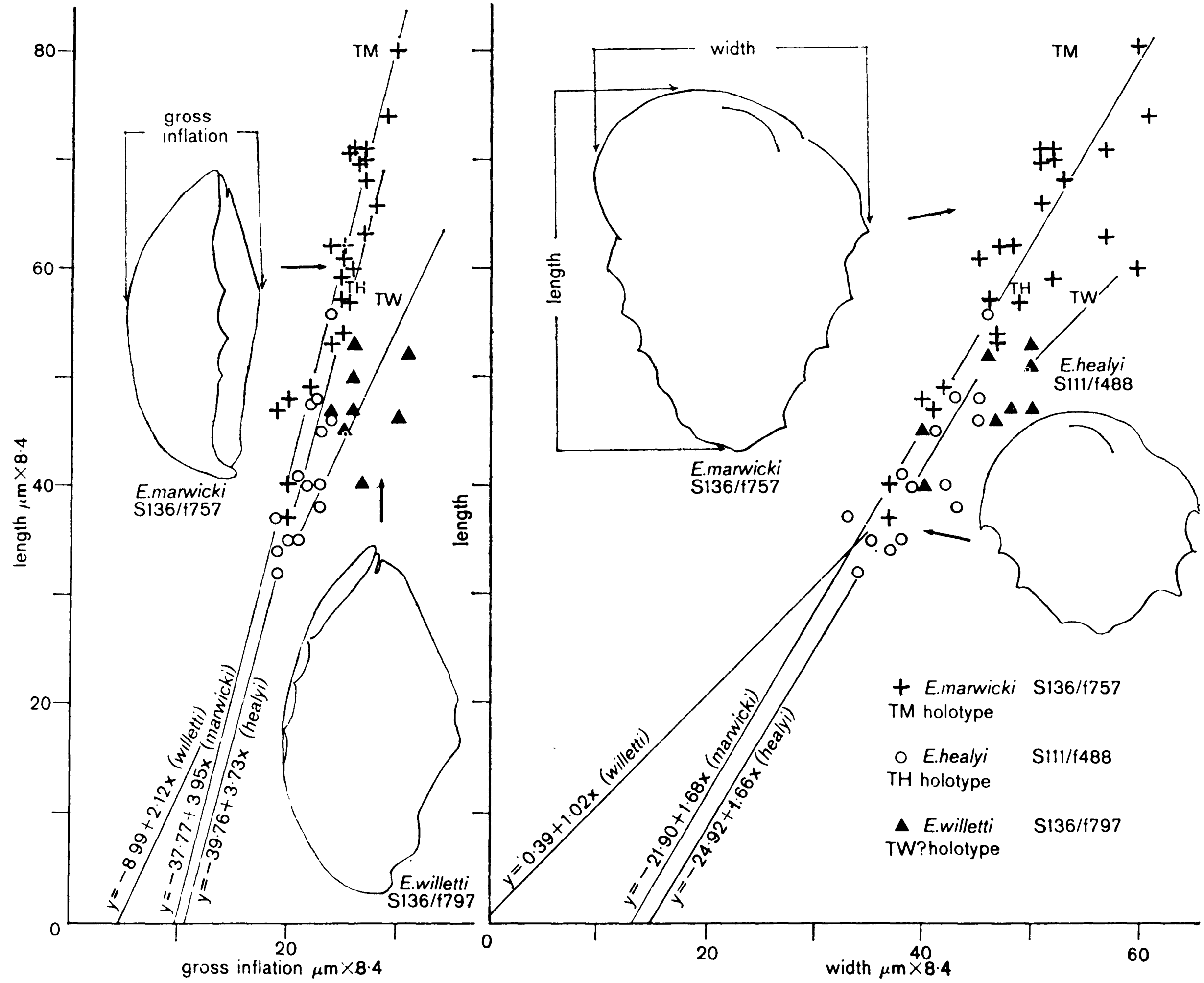

Figure 10.4 Analysis of variability in *Ehrenbergina marwicki*, *E. willetti* and *E. healyi*. Length is plotted against gross inflation and against width. From Scott (1973c). The formula for the straight line or reduced major axis is $Y = ax + b$, where x = length, Y = length/width, a = growth ratio, and b = initial growth index

tain an impoverished and stunted fauna. *Bolivina* and *Brizalina* are least affected, followed by *Cassidulina* and *Epistominella*. *Bolivina* and *Brizalina* appear to be able to tolerate levels as low as 0.10 ml/l (Boltovskoy, 1972).

Traced from the Shelf on to the Slope the Buliminida, especially *Bolivina*, *Bulimina* and *Uvigerina*, show marked morphological trends (Bandy, 1960a). The Shelf species are less ornamented and there is progressive increase and differentiation of surface sculpture down the Slope (figure 10.5). Bathyal species are also larger, as has been noted earlier in the case of other groups. These trends have been confirmed by the work of Patsy Smith (1963), Lutze (1964) and Boersma (1977). They also occur at the infraspecific level and *Bolivina argentia*, studied by Lutze, shows an increase in overall length, strength of costae and length of initial spine down the Slope.

The complexity of the environment, and the care with which the microfaunas of the Slope must be interpreted, is emphasised by recent work. Assemblage zones tend to be more marked than in the Abyss or on the Shelf. This is explained as the result of 'intense resource competition' accentuated in certain areas by restricting, low oxygen levels (Rowe and Haedrich, 1978). The Upper Slope fauna is transitional between seasonally variable Shelf conditions with high rates of recycling of organic matter and the non-seasonal Abyss with low rates of recycling. The biomass

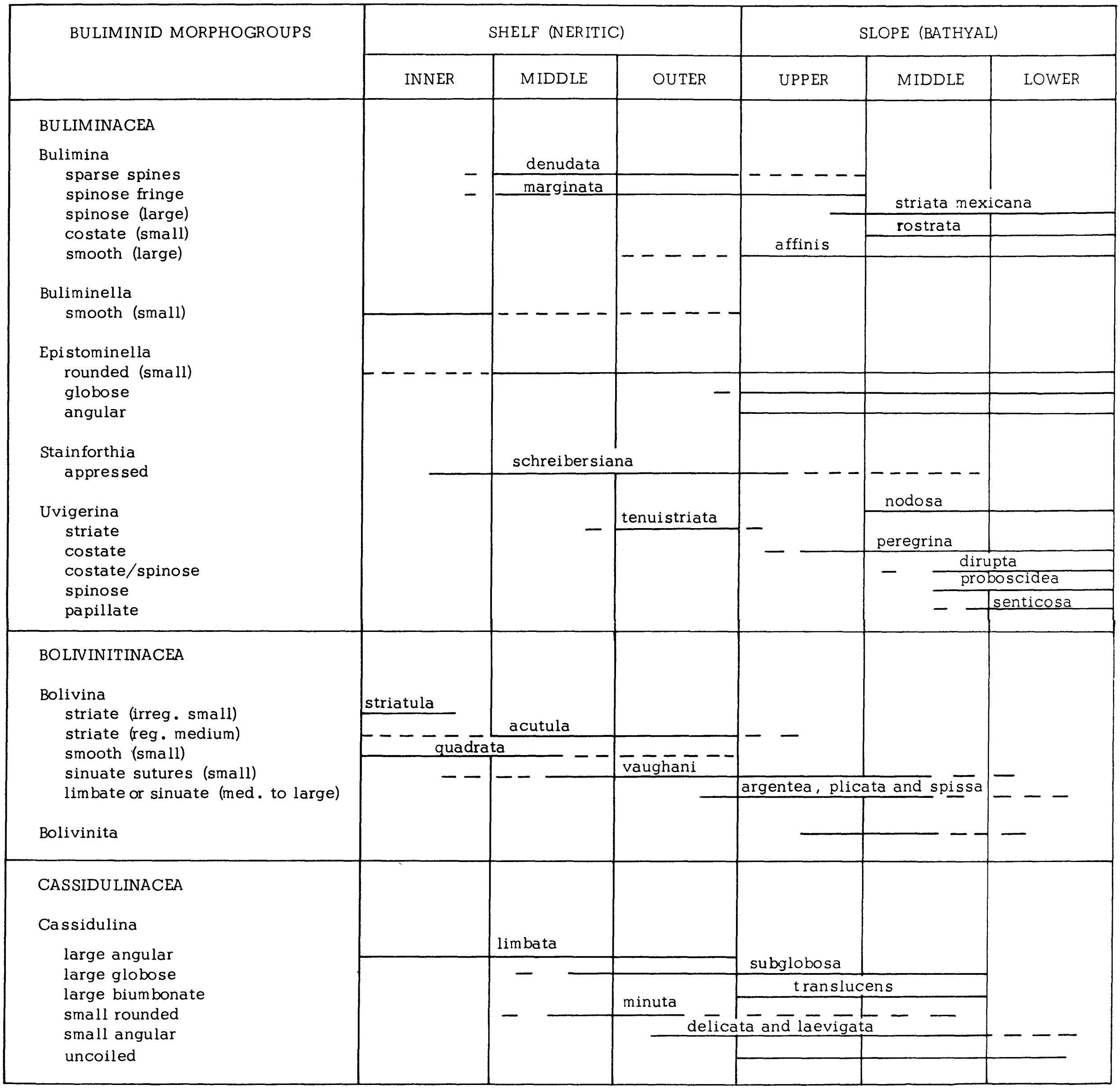

Figure 10.5 Distribution of morphogroups of buliminids in the modern oceans. After Bandy (1960a)

decreases exponentially with depth, and selection favours species that can find and utilise packaged detritus such as faecal pellets and carcases. The Buliminida are, perhaps, specially adapted to exploit organic detritus of this sort.

An important discovery of Rowe and Haedrich is that whereas benthic fish dominate between 1000 and 1400 m, the fauna becomes dominated by echinoderms at mid-Slope. In the Slope and Basin area off California, Douglas and Heitman (1978) find that the mud-eating macrobenthos, including echinoderms, is limited by low oxygen levels. This leads to the paradoxical result that the standing crop of living forams in the oxygen minimum area is 100/cm^3, whereas it is only ±1/cm^3 in the high oxygen areas due to control by the macrobenthos. This underlines the importance of the adaptation of buliminids to low oxygen levels.

A further important factor is that bottom currents are most active at the Shelf break (off New England, Ross and MacIlvaine, 1978). This may cause winnowing and concentration of dead tests and also movement down the Slope.

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SUMMARY CLASSIFICATION

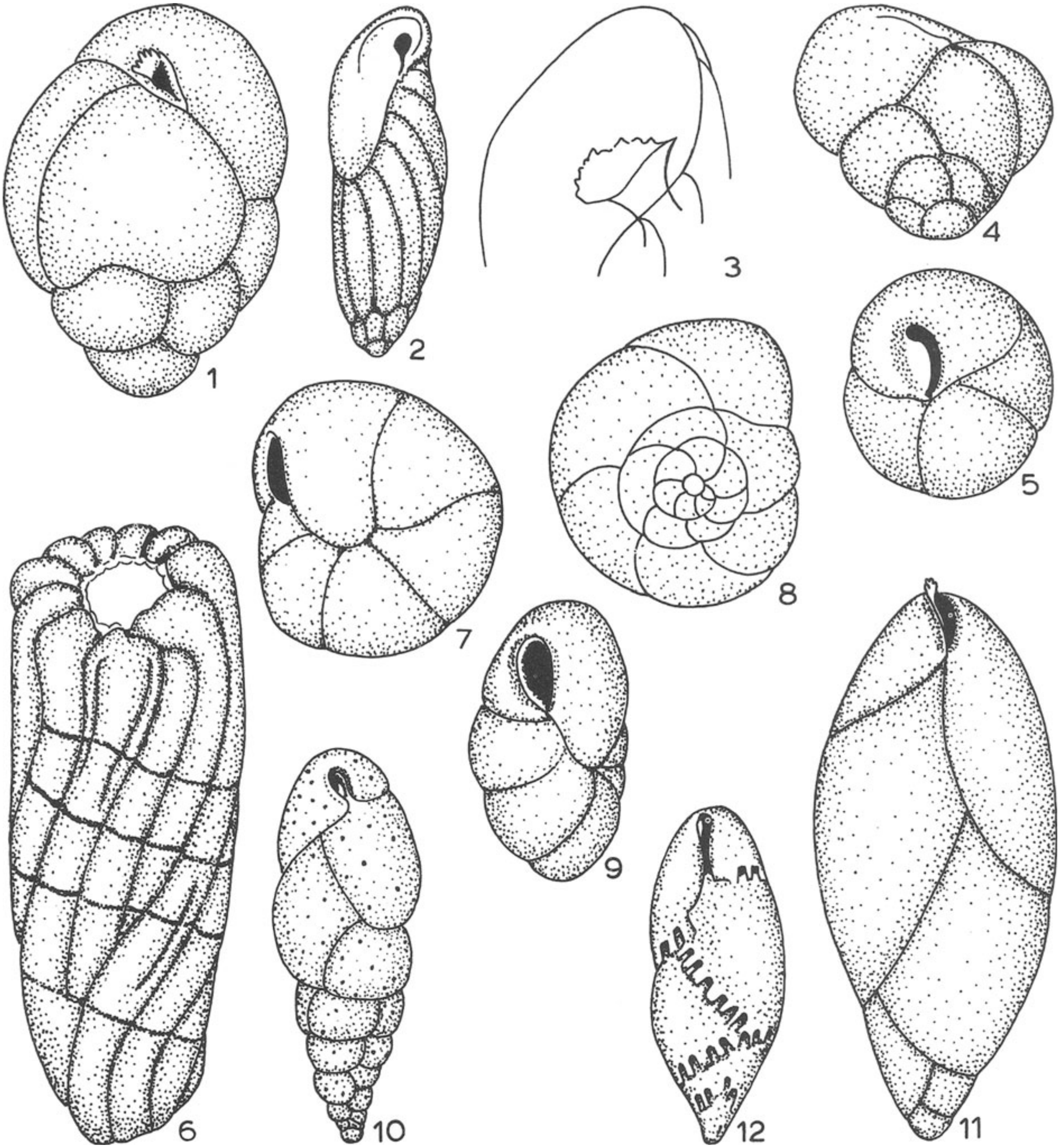
MAIN FAMILIES AND IMPORTANT GENERA OF BULIMINIDA

BULIMINIDA	wall hyaline, oblique or radial, bilamellar; aperture characteristically comma-shaped or a slit, terminal and produced in advanced forms, with internal toothplate connected to previous foramen; Jur. – Rec. Key figures 10.6 and 10.7.
BULIMINACEA	trochospiral to triserial, biserial and uniserial; aperture umbilical, basal or comma-shaped, terminal in advanced forms, may be replaced by multiple openings or trematophore; broad toothplate with free border that may join anterior end of aperture; most genera hyaline radial; Jur. – Rec. Key figure 10.6.
BULIMINIDAE	triserial to biserial and uniserial; aperture comma-shaped or terminal and round; Jur. – Rec.
Bulimina (no. 10)	triserial; aperture extending into apertural face from basal suture; toothplate with produced or rolled-up free border; Pal. – Rec. (simple trough-like tooth = *Praebulimina,* Mid. Jur. – U. Cret.; trigonal also = *Pyramidina,* U. Cret.; biserial in adult also = *Neobulimina,* Cret.; biserial to uniserial also = *Rectobulimina,* Cret.).
Praeglobobulimina (no. 11)	triserial with globular, strongly overlapping chambers; aperture extending up from basal suture; free edge of toothplate folded and joined to anterior end of aperture, tip protrudes like cockscomb; Pal. – Rec. (terminal aperture and toothplate double folded = *Globobulimina*).
Stainforthia (no. 13)	narrowly elongate, triserial (at least in B form) to twisted biserial; aperture narrowly comma-shaped in marked depression; flaring toothplate with serrated free edge; Eoc. – Rec. (hyaline oblique without apertural depression = *Fursenkoina,* U. Cret. – Rec.; simple trough-like tooth also = *Cassidella,* U. Cret. – Rec.).
Virgulinella (no. 12)	triserial to biserial with retral processes and sutural pores; aperture extending up from basal suture with reduced toothplate; Neo. (porous trematophore but toothplate absent = *Delosina,* Rec.).
TURRILINIDAE	trochospiral with more than 3 chambers to the whorl; aperture high arch or comma-shaped; toothplate simple, trough-like or cornet-shaped; U. Cret. – Rec.
Turrilina (no. 1)	high trochoid with 4 chambers in each whorl, globular; aperture a high arch; Eoc. – Olig.
Buliminella (nos. 2/3)	numerous high chambers in drawn-out spiral; aperture comma-shaped in depression; toothplate with saw edge; U. Cret. – Rec. (aperture terminal, round = *Buliminellita,* Eoc. – Mio.; aperture cribrate and toothplate lost = *Sporobuliminella,* U. Cret.).
Buliminoides (no. 6)	low chambers in drawn-out spiral coiled round open umbilicus—formed by resorption in adult; Olig. – Rec.

Baggatella (nos. 4/5)	low trochoid with narrowly comma-shaped aperture extending from umbilicus into apertural face; Eoc. – Rec. (aperture parallel to periphery = *Epistominella* (nos. 7 – 9), Pal. – Rec.; trochoid to triserial = *Caucasina,* U. Cret. – Mio.).
UVIGERINIDAE	triserial to biserial or uniserial; aperture terminal with neck; simple toothplate; U. Cret. – Rec.
Uvigerinella (no. 16)	triserial, aperture subterminal with high collar, connected by suture to basal suture; Pal. – Rec.
Uvigerina (no. 14)	triserial, aperture produced with phialine lip; toothplate with flaring free edge; Eoc. – Rec. (biserial adult = *Hopkinsina;* triangular in section = *Pseudouvigerina,* U. Cret.).
Trifarina (no. 15)	triserial to uniserial, triangular with keeled margins; U. Pal. – Rec. (round in section = *Rectuvigerina,* M. Eoc. – Rec.; triserial to biserial and uniserial also = *Elhasaella* Haman (1978), Maas.; uniserial chambers loosely attached = *Siphouvigerina* (no. 17), Olig. – Rec.; triserial initial part only in B form = *Siphogenerina,* Eoc. – Rec.).
PAVONINIDAE	triserial to biserial and uniserial, uniserial chambers triangular or strongly arched; simple toothplate, lost in adult; aperture multiple in advanced forms; Eoc. – Rec.
Reussella (no. 18)	triserial, sharply angular; aperture a basal slit with cornet-shaped toothplate; Eoc. – Rec. (cribrate = *Fijiella,* Rec.).
Chrysalidinella (no. 20)	triserial to uniserial, triangular or quadrangular; aperture terminal, multiple; toothplate lost in uniserial part; Eoc. – Rec. (uniserial part round in section = *Tubulogenerina,* Eoc. – Mio.).
Pavonina (no. 19)	triserial to biserial and uniserial with high arched chambers; aperture replaced by multiple pores, no toothplate; Mio – Rec.
BOLIVINITACEA n. superfam.	compressed biserial to uniserial (rarely with planispiral initial part) or enrolled biserial to uncoiled; aperture comma-shaped or a slit in the plane of compression, becoming terminal and produced in advanced forms; toothplate simple, trough-like or cornet-shaped, wall usually hyaline radial; Jur. – Rec. Key figure 10.7.
BOLIVINITIDAE	compressed biserial to uniserial (rarely with planispiral initial part); aperture extending into aperture face from basal suture or terminal and rounded; Jur. – Rec.
Brizalina (nos. 2/3)	biserial often carinate, chambers wide and low; apertural slit runs into apertural face from basal suture; toothplate trough-like; Jur. – Rec. (with retral processes and sutures crenulate = *Bolivina* (no. 1), U. Cret. – Rec.; rhomboidal with strong longitudinal costae = *Bolivinoides* (nos. 4/5), U. Cret.; planispiral initial part = *Spirobolivina,* Pal. – Eoc.).
Bolivinita (nos. 6/7)	biserial, much compressed with flat or concave sides and truncate periphery; Mio. – Rec.

Rectobolivina (no. 8)	biserial to uniserial and only slightly compressed; aperture terminal and rounded; M. Eoc. – Rec.
EOUVIGERINIDAE	biserial to uniserial; aperture terminal, produced with neck and lip; L. Cret. – Rec.
Eouvigerina (no. 9)	biserial, final chamber central; aperture with crenulate inner margin; Alb. – Eoc.
Siphogenerinoides (nos. 10/11)	biserial to uniserial and round in section; aperture oval or reniform (with toothplate visible at side); U. Cret. – Pal.
Siphonodosaria (no. 12)	uniserial, aperture with crenulate inner margin; Eoc. – Rec. (aperture reniform = *Stilostomella,* Cret. – Rec.).
ISLANDIELLIDAE	enrolled biserial to uncoiled; aperture in median line or subterminal with cornet-shaped toothplate; Cen.
Islandiella (nos. 13/14)	close-coiled with rounded periphery; toothplate with triangular free tip; Cen. (uncoiled in adult with subterminal aperture = *Cassidulinoides* (no. 15), U. Eoc. – Rec.; uncoiled, round in section with irregular chambers = *Orthoplecta,* Rec.).
Ehrenbergina (nos. 16 – 18)	compressed carinate, enrolled biserial to uncoiled triangular; Eoc. – Rec.
CASSIDULININACEA	triserial to biserial and uniserial or enrolled biserial to uncoiled; aperture subterminal or near periphery in plane of compression usually with dentate lower or outer margin; toothplate a free siphon, reduced or lost in advanced forms, most genera hyaline oblique; L. Cret. – Rec. Key figure 10.7.
PLEUROSTOMELLIDAE	triserial to biserial and uniserial or unilocular, chambers embracing; aperture subterminal to terminal, crescentic or chevron-shaped, characteristically with dentate lower border; internal siphon connects upper border with previous foramen; L. Cret. – Rec.
Wheelerella (nos. 19/20)	compressed triserial to biserial and uniserial; aperture subterminal, crescentic with broad tooth; U. Cret. (rounded and aperture subterminal beneath hood with two triangular teeth = *Bandyella*).
Pleurostomella (nos. 21/22)	biserial to uniserial in the adult, elongate and round in section; aperture subterminal beneath hood with two triangular teeth; ?L. Cret. – Rec. (aperture crescentic with broad tooth = *Ellipsoidella*; aperture cribrate = *Cribropleurostomella* Owen 1971, U. Cret.; uniserial throughout = *Nodosarella* (nos. 25/26), Cen.).
Ellipsopolymorphina (no. 27)	biserial to uniserial, chambers strongly inflated and embracing; aperture chevron-shaped with spatulate tooth; Neo. (chambers completely overlapping = *Ellipsobulimina*).
Ellipsoglandulina (nos. 23/24)	uniserial, chambers inflated and strongly overlapping, round in section; aperture crescentic with broadly spatulate tooth; Eoc. – Rec. (chambers completely overlapping, aperture terminal = *Ellipsolingulina* (nos. 28/29), Palaeogene).
Parafissurina (nos. 30/31)	unilocular; aperture subterminal beneath hood, crescentic with broad tooth; siphon attached to rear wall;

	hyaline radial; M. Eoc. – Rec. (aperture a terminal slit without tooth; siphon usually projecting freely into interior = *Fissurina*).
CASSIDULINIDAE	enrolled biserial to uncoiled or streptospiral; aperture a curved slit parallel to the periphery with broad, low tooth on outer border; toothplate reduced to short plate projecting in from inner border, or absent; Eoc. – Rec.
Cassidulina (nos. 32/33)	enrolled biserial, compressed carinate; Eoc. – Rec. (honeycomb ornament = *Favocassidulina,* Rec.; rounded periphery = *Globocassidulina*).
Sphaeroidina (no. 34)	streptospiral and sub-globular; aperture crescentic and almost closed off by broad rounded tooth, near basal suture; toothplate absent; hyaline radial; U. Eoc. – Rec.



Key figure 10.6 **Buliminida, Buliminacea**
1 *Turrilina brevispira*, **Dam, after Hansen, × 312**
2/3 *Buliminella elegantissima* **(d'Orbigny); 2 after L. & T., × 200**
3 toothplate after Hofker, × 500
4/5 *Baggatella inconspicua* **Howe; 4 side view, 5 ventral view, × 300**
6 *Buliminoides williamsonianus* **(Brady), after Hofker, × 450**
7–9 *Epistominella vitrea* **Parker, after Haynes; 7 ventral view, 8 dorsal view, 9 side view, all × 320**
10 *Bulimina thanetensis* **Cushman & Parker, after Haynes, × 120**
11 *Praeglobobulimina ovata* **(d'Orbigny), after Haynes, × 120**
12 *Virgulinella pertusa* **(Reuss), after L. & T., × 64**

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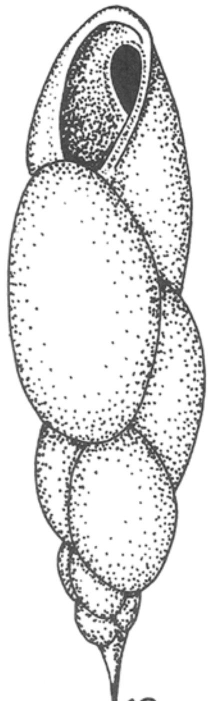
Key figure 10.6 ***(continued)***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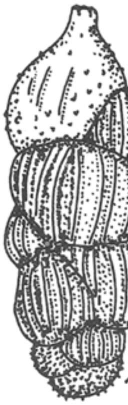
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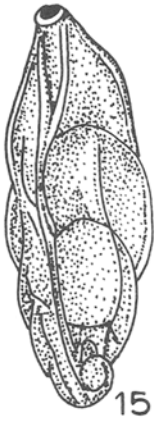
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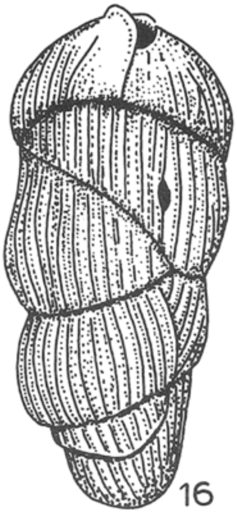
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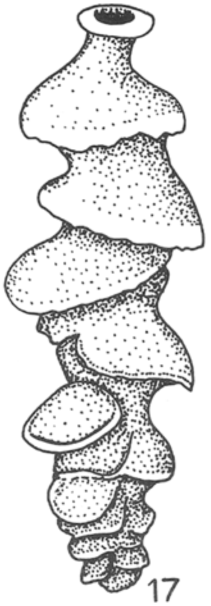
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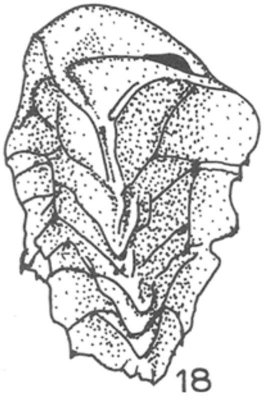
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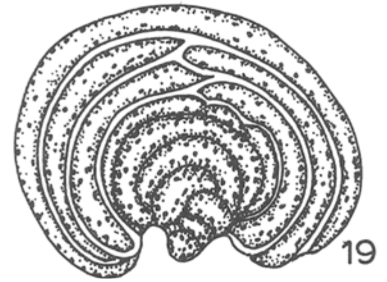
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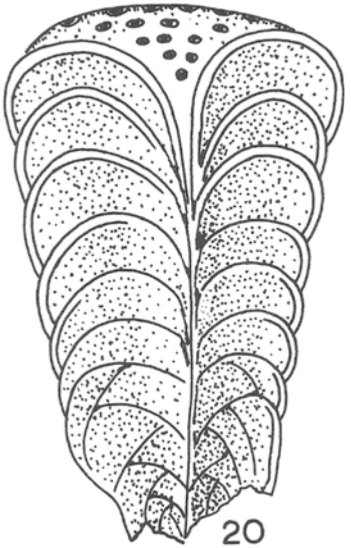
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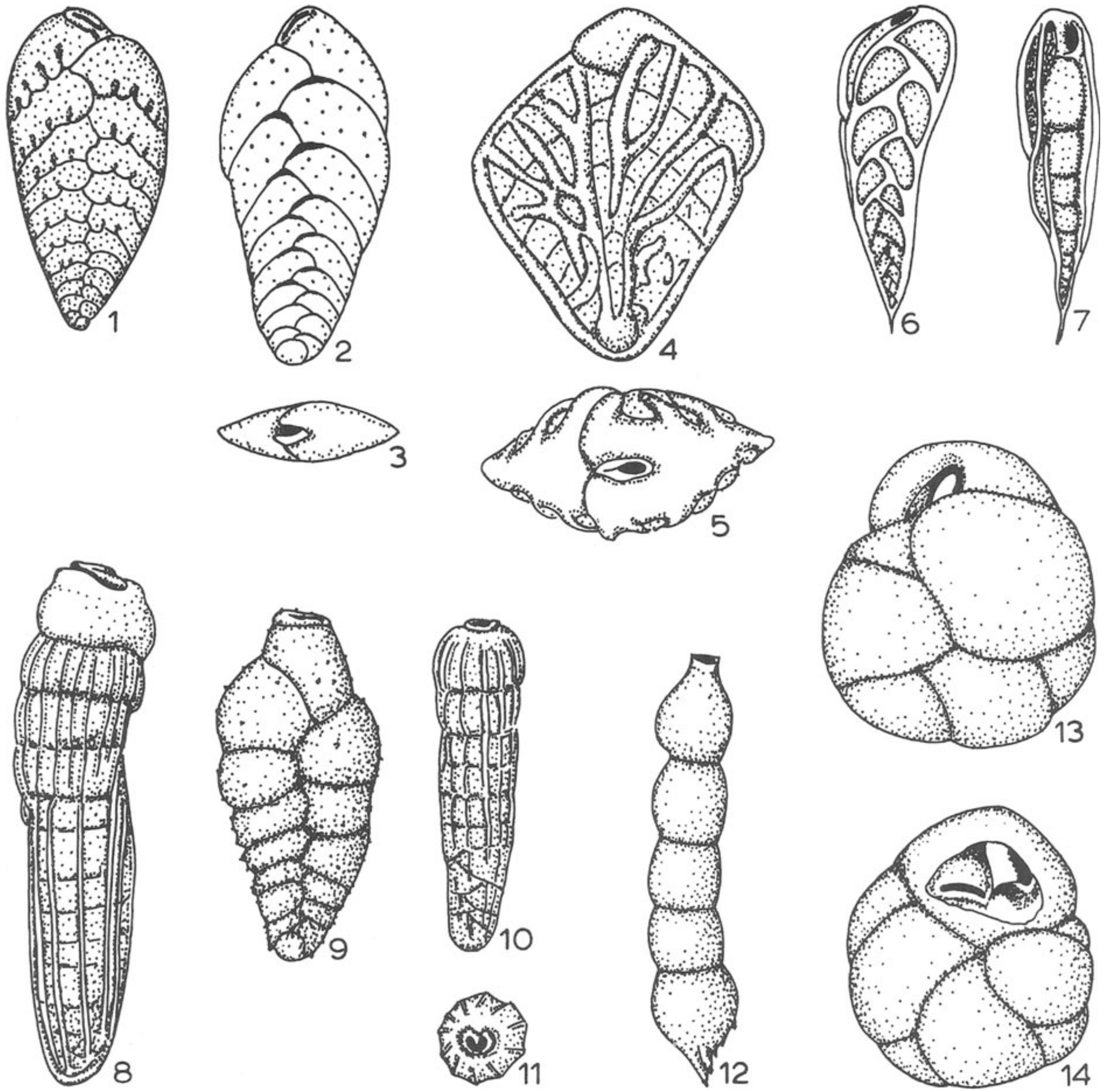
13 *Stainforthia concava* (Höglund), × 200
14 *Uvigerina pygmaea* d'Orbigny, after L. & T., × 94
15 *Trifarina angulosa* (Williamson), after L. & T., × 83
16 *Uvigerinella oveyi* Haynes, × 200
17 *Siphouvigerina fimbriata* (Sidebottom), after L. & T., × 185
18 *Reussella spinulosa* (Reuss), after L. & T., × 100
19 *Pavonina flabelliformis* d'Orbigny, after Brady, × 60
20 *Chrysalidinella dimorpha* (Brady), after L. & T., × 140



Key figure 10.7 Buliminida, Bolivinitacea

1 *Bolivina robusta* **Brady, × 100**

2/3 *Brizalina spathulata* **(Williamson), side and apertural views, after Haynes, × 100**

4/5 *Bolivinoides draco* **(Marsson), side and apertural views, after Montanaro Gallitelli, × 100**

6/7 *Bolivinita quadrilatera* **(Schwager), side and edge views, after Brady, × 35**

8 *Rectobolivina raphana* **(Parker & Jones), after L. & T., × 55**

9 *Eouvigerina zelandica* **(Finlay), after Montanaro Gallitelli, × 180**

10/11 *Siphogenerinoides plummeri* **(Cushman), side and apertural views, after Montanaro Gallitelli, × 66**

12 *Siphonodosaria abyssorum* **(Brady), after L. & T., × 22**

13/14 *Islandiella islandica* **(Nørvang); 13 side view, 14 internal view to show toothplate, × 50**

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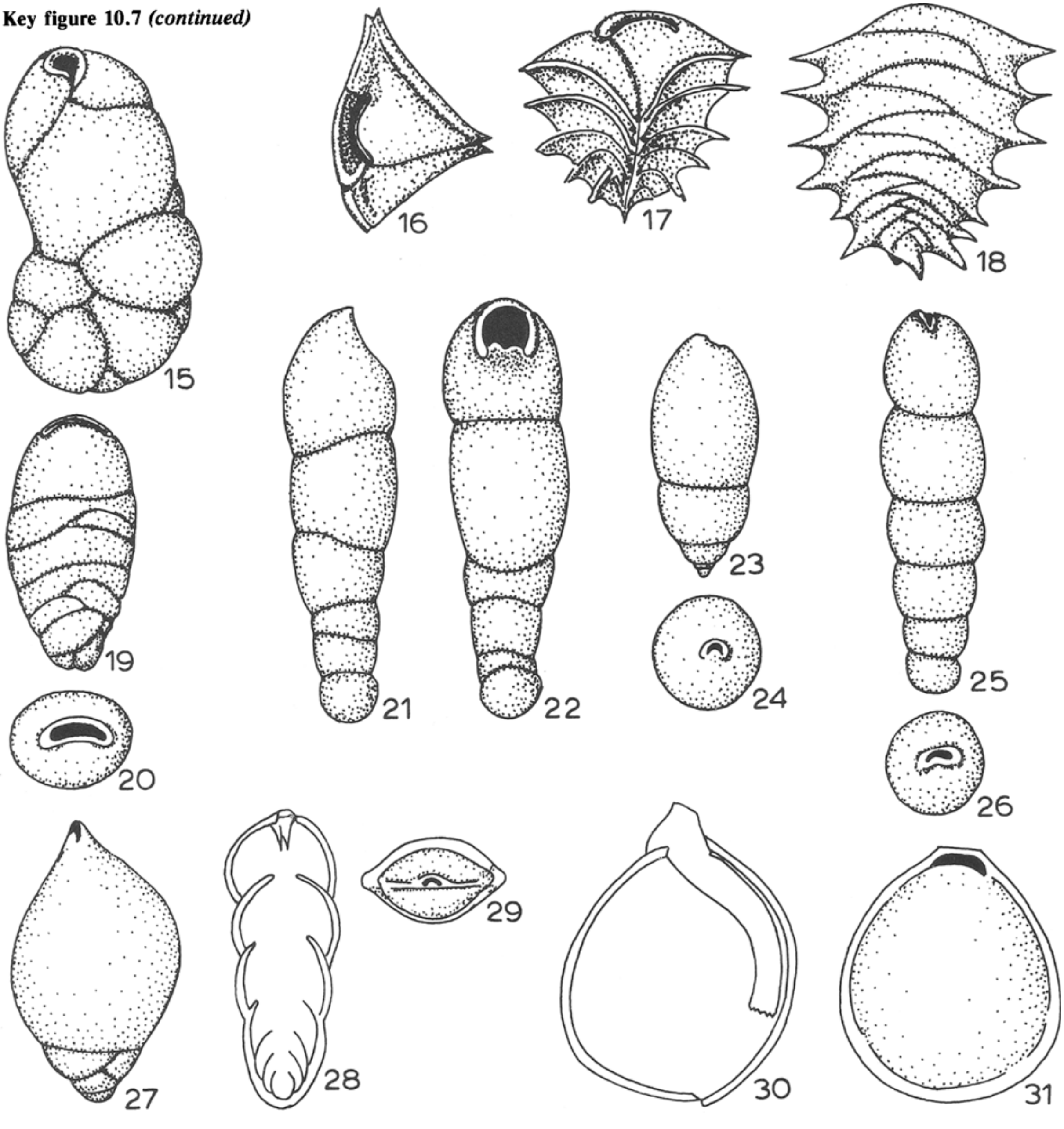
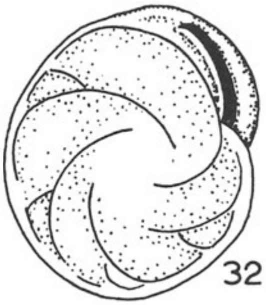
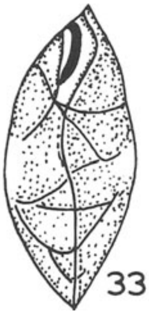
Key figure 10.7 ***(continued)***

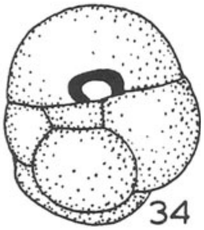


15 ***Cassidulinoides parkerianus*** **(Brady), after L. & T., × 150**
16 – 18 ***Ehrenbergina pacifica*** **Cushman, apertural, front and rear views, after Brady, × 60**
19/20 ***Wheelerella magdalensis*** **Petters, side and front views, after L. & T., × 100**
21/22 ***Pleurostomella subnodosa*** **(Reuss), side and front views, after L. & T., × 75**
23/24 ***Ellipsoglandulina laevigata*** **Silvestri; side and apertural views, × 44**
25/26 ***Nodosarella rotundata*** **(d'Orbigny), side and apertural views, after L. & T., × 36**
27 ***Ellipsopolymorphina schlichti*** **(Silvestri), × 50**
28/29 ***Ellipsolingulina silvestri*** **Galloway, side and apertural views, × 150**
30/31 ***Parafissurina ventricosa*** **(Silvestri), internal and apertural views, × 55**

Key figure 10.7 *(continued)*







32/33 *Cassidulina laevigata* **d'Orbigny, side and edge views, after L. & T., × 78**
34 *Sphaeroidina bulloides* **d'Orbigny, apertural view, after Vășíček, × 44**

Chapter 11

The Robertinida

> We continually overrate the perfection of the geological record and falsely infer, because certain genera or families have not been found below a certain stage, that they did not exist before that stage.
>
> (Darwin, 1859)*

The hyaline Foraminifera exploit all the preferred crystallographic orientations of *calcite* in the construction of their tests and also include the Robertinida, a group with glassy tests built of radially arranged, pseudohexagonal twins of *aragonite*—see chapter 4. They first appear in the Middle Triassic and range down to the present day.

Many robertinids were included previously with the buliminids because of similarities in apertural form, presence of internal structures and occurrence in deep-water environments. However, as well as being sharply distinct in wall structure, their apertures and internal structures prove to be significantly different also, when closely examined.

The aperture in the Buliminida is characteristically a comma-shaped opening running up into the apertural face, or terminal, with a trough-like or cornet-shaped toothplate. In the Robertinida, the aperture characteristically opens beneath an umbilical flap with extensions along the basal suture (distal arch) and into the apertural face (proximal notch or slit). The internal structures are usually more complex than in the Buliminida and in advanced forms the toothplate is developed as an almost complete partition, cutting off a 'supplementary chamberlet', visible from the exterior. Although peripheral and terminal apertures appear in some families, the majority of genera are low trochoid and terminal apertures are not developed. Similar apertures are exhibited by *Discorbis* and *Rosalina* (Discorbacea) but these genera are calcitic and lack internal structures.

The morphological features shown by the Robertinida, together with their unusual wall structure, are a strong indication that they constitute a natural group.

The tendency for aragonite to go into solution in sea water, especially below 200 m, means that this group is inevitably less well known than the orders of calcitic Foraminifera. The micropalaeontologist is faced with the same problems as the worker on aragonitic molluscs. The shell may be replaced by the more stable calcite or, more commonly, dissolved away, sometimes leaving a cast. However, as in the case of the ammonites, pyritic casts may be quite revealing of the inner structure.

In these circumstances of aggravated imperfection of the fossil record, the tracing of phylogenetic relationships is fraught with difficulty. One of the earliest known genera is the Middle Triassic *Duostomina*. It had been regarded as the ancestral rootstock from which the other members of the group have descended. But detailed investigation has revealed an extremely complicated, internal partition, worthy of comparison with the contrapuntal forms of modern sculpture (figure 11.1). This suggests that *Duostomina* is a specialised genus with a long history of development still undetected and an unlikely ancestor for later robertinids.

Another problem is the position of the so-called Triassic and Jurassic 'Globigerinas'. In the last decade they have been placed near *Oberhauserella*. Further work, especially on their wall structure, is required to firmly establish their taxonomic relationships and to decide whether all of them belong in the Robertinida.

CHAMBER FORM AND COILING MODES

As is to be expected from the susceptibility of the aragonitic test to solution, this order is the smallest among the Foraminifera, reaching only 3 per cent of the total, as shown by the table in

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**The Origin of Species*, 6th edn (reprint 1945), Watts, London.

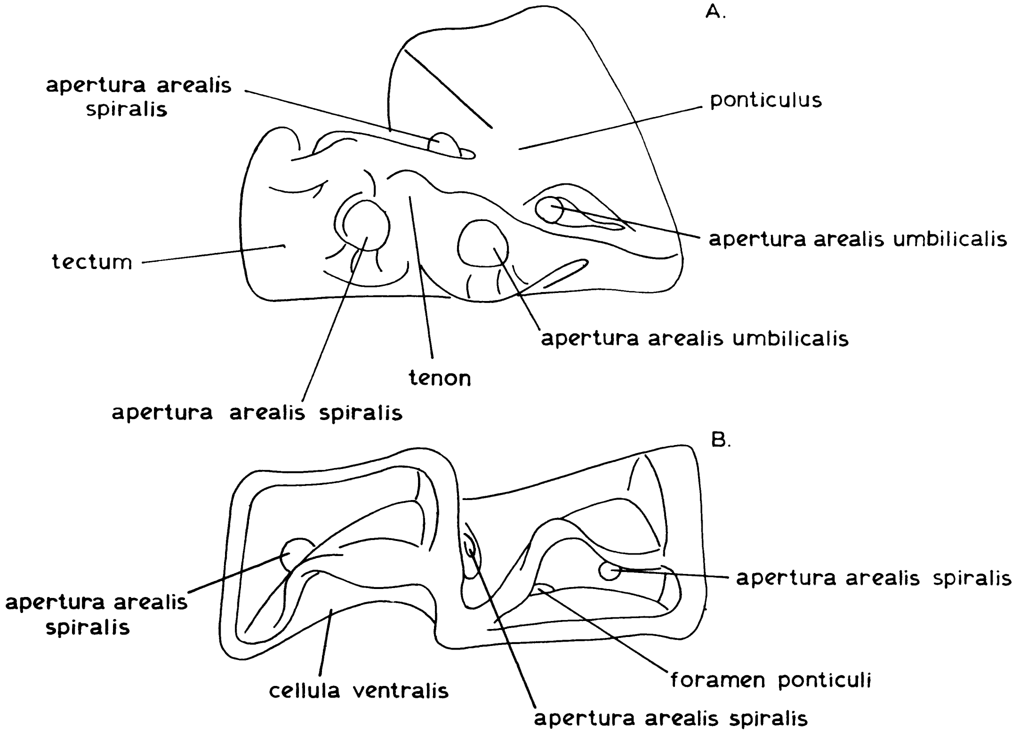

A.
apertura arealis spiralis
ponticulus
apertura arealis umbilicalis
tectum
apertura arealis umbilicalis
tenon
apertura arealis spiralis
B.
apertura arealis spiralis
apertura arealis spiralis
foramen ponticuli
cellula ventralis
apertura arealis spiralis

Figure 11.1 Internal structure of *Duostomina biconvexa,* drawn from models constructed by Edith Kristan-Tollmann (1966). A external view of aperture, B view of partition and apertures from inside. Both views dorsal side upwards. Note that the lobe between the apertures, which are considered areal, is referred to as a tenon. The two openings are referred to as spiral (outer or proximal) and umbilical (inner or distal) in position. The internal foramina are given the same nomenclature

figure 4.3. Although the Duostominacea are now included here and a number of new genera have been added since the publication of the 'Treatise' (1964), especially by Fuchs (1973), this hardly affects the percentage. There are no attached forms and the great majority are low trochospiral (86 per cent), although this figure is exaggerated by inclusion of those genera which become uncoiled and auriculate in the adult. If these are considered high trochoid the figure falls to nearer 60 per cent. Otherwise, the number of high trochospiral as well as planispiral genera (except in the Duostominacea) is very low.

The superfamilies and families are recognised upon the basis of chamber arrangement, aperture form and as far as our meagre knowledge allows upon the presence and development of a tooth-plate or internal partition. See the Summary Classification at the end of the chapter.

Duostominacea

Discrimination of the families in this superfamily is difficult both because of the imperfection of the fossil record and because of lack of knowledge of internal structures. Edith Kristan-Tollmann (1966) has described the elaborate partition in *Duostomina* (figure 11.1) but, so far, comparable structures have not been described from other genera in this group. The Duostominidae are therefore distinguished on the basis of their distinctive, crenulate, double aperture. There are numerous chambers in a trochospiral coil with evolute dorsal side and involute ventral side. The umbilicus may be open or closed. Involute trochospiral to asymmetric, planispiral genera with single arched aperture, almost in the median line, are included in the Asymmetrinidae. The aperture is again markedly crenulate.

Low to high trochospiral genera with open or only partially closed umbilicus and relatively few, often globular, chambers in the last whorls are included in the Oberhauserellidae. There is considerable variation in apertural form and while *Oberhauserella* has a lobe with distal arch and proximal fold other genera show simple umbilical and extra-umbilical apertures, which has led to their confusion with members of the Globi-

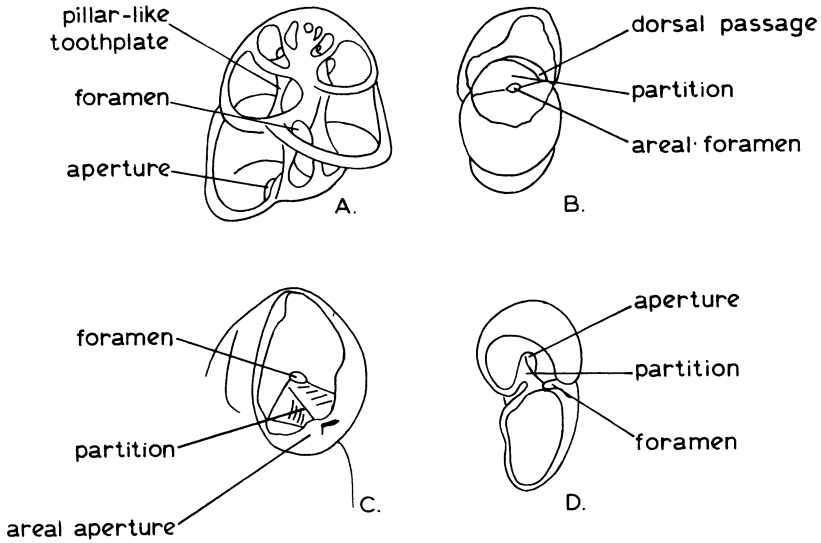


Figure 11.2 Toothplates and partitions in robertinids. A pillar-like toothplate in *Conorboides mitra,* after Hofker; B partition and dorsal passage in *Ceratolamarckina tuberculata,* after Haynes; C inverted V-shaped partition and areal aperture in *Alliatina excentrica,* after L. & T.; D folded partition in *Robertina arctica,* after L. & T.

gerinacea. Fuchs (1973) has distinguished a number of new taxa, including *Tectoglobigerina* where the aperture is partially filled with a plate. These probably represent more than one family.

Ceratobuliminacea

Genera with narrow toothplate or partition partially blocking communication between the aperture and the foramen, developed secondarily by resorption, are grouped in the superfamily Ceratobuliminacea. This includes the Conorboididae, with closed umbilicus and pillar-like toothplate (figure 11.2A), the Epistominidae in which the aperture has become a slit along or parallel to the periphery and the Ceratobuliminidae which are deeply umbilicate with characteristically notched, umbilical aperture and highly developed partition (figure 11.2B).

As noted by Grigelis (1978b) the relationship of *Lamarckella, Praelamarckella* and *Pseudolamarckina,* hitherto placed in the Ceratobuliminidae, together with *Reinholdella,* are still uncertain, as wall structure and internal structures are unknown. Previous authors have also had difficulty in the attempt to distinguish *Hoeglundina* from *Epistomina,* now taken to include both *Brotzenia* and *Voorthuysenia,* Hofker 1954.

The Cenozoic genera, *Stomatorbina, Mississippina* and *Schlosserina,* were included in the Epistominidae in the 'Treatise' but differ in possessing ventral umbilical to extra-umbilical, median and cribrate apertures, respectively. There are bands of clear shell material parallel to the periphery, on both sides in *Mississippina,* considered to represent the former presence of marginal slits, homologous with those in *Epistomina.* Probably these should be placed in a separate family. The internal structures are not known and the wall structure is uncertain in *Schlosserina.*

Robertinacea

This superfamily is distinguished by the presence of supplementary chamberlets produced by infolding of the wall. Here the foramen develops at least in part from the primary aperture and is thus, unlike the foramen in the Ceratobuliminacea, an homologous structure. In the Robertinidae, which are high trochospiral or low trochospiral to asymmetrically uncoiled, the aperture is umbilical and characteristically opens beneath a lobe and has proximal and secondary sutural extensions. In *Robertina,* the opening is reduced to a vertical slit but there is a supplementary aperture at the junction of secondary and basal sutures on the reverse side (figure 11.2D).

In the Alliatinidae the proximal extension of the aperture becomes closed off to give an oval, areal aperture and the partition is an inverted-V or chevron structure (figure 11.2C). Chamber arrangement is low trochospiral to planispiral and in *Cushmanella* which has the partition reduced to an inverted split-tube, there is a poreless zone above the areal aperture. The split-tube in this genus resembles the trough-like siphon in *Colomia* and *Ungulatella* which were included in this group in the 'Treatise'. However, as the wall structure of these genera is unknown and they are without supplementary chamberlets, further work is clearly required before they can be placed in the Robertinida with any confidence.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

As explained, the relatively sparse fossil record of this order means that phylogenetic relationships are in doubt. They must also remain largely speculative in the absence of knowledge of tooth-structures in Triassic and Jurassic forms. There has been considerable debate over whether the epistominids or the ceratobuliminids are the most primitive and over the origin of the aragonitic group.

Hofker (1956) considered that the Epistominidae and Ceratobuliminidae sprang separately from the agglutinated Valvulinidae and that *Hoeglundina* gave rise to *Robertinoides* and the *Robertinidae.* A quite different origin within the microgranular fusulinids was suggested by Loeblich and Tappan (1974) but again with two separate lines, one from the Endothyridae to the Asymmetrimidae and one from the Tetraxidae to the Duostominidae. The Duostominidae are then considered to have been ancestral to the Ceratobuliminicea via the Oberhauserellidae.

The most primitive and earliest ceratobuliminids appear to be the Conorboididae, and Brotzen (1963) thought that *Duostomina* gave rise directly to *Reinholdella.* However, since the discovery of the complex partition in *Duostomina,* noted above, an alternative line of descent from *Diplotremina* through the Oberhauserellidae to *Reinholdella* has been preferred (Fuchs, 1967, 1973). *Diplotremina* has an open umbilicus and is apparently without toothplate but the crenulate, double aperture seems more advanced than the arch and proximal notch in *Oberhauserella.*

The student should note that we have to be careful not to read the stratigraphical record, in which the more abundant genera and species figure most prominently, as necessarily indicating a straightforward line of evolutionary descent. As a general rule in evolutionary studies we find (as with mammals) that new groups arise from relatively unspecialised, conservative stocks, whereas highly specialised forms are, generally, end members that disappear without further issue. Again, it is not impossible that aragonitic wall structure has arisen more than once but it seems unlikely that it could have arisen twice from compound, microgranular families. An origin from within the Ataxophragmiacea is perhaps most likely.

Epistomina appeared in the Middle Jurassic, possibly from among the Conorboididae. Rapid development of a true partition with ventral suture, *Epistominita* and *Epistominoides,* and an uncoiling trend, *Rectoepistominoides,* took place before the end of the Jurassic.

The Ceratobuliminidae may have descended separately from the Oberhauserellidae in the late Jurassic, remaining deeply umbilicate with notched umbilical aperture but developing a complex partition below a secondary areal foramen. Most genera are present by the Upper Cretaceous but further development took place in the Cenozoic with appearance of *Ceratocancris* in the Miocene.

The antecedants of the Cenozoic Robertinacea are unknown but the Robertinidae possibly originated from the Ceratobuliminidae via *Pseudobulimina* in the Eocene and show strong uncoiling trends from low trochospiral to auriculate. The family Alliatinidae made a late appearance in the Neogene, probably from *Geminospira.* Here the proximal extension of the aperture into the face of the chamber is pinched off to become areal, and coiling becomes planispiral in *Alliatina* and *Cushmanella.*

STRATIGRAPHIC USE OF THE ROBERTINIDA

Despite relatively low numbers and difficulties because of poor preservation, the continuous evolutionary development of the robertinids makes them useful in biostratigraphy. This applies particularly in the early Mesozoic where other glassy Foraminifera apart from the nodosariids are rare.

The Duostominidae, Middle Triassic, and Asymmetrinidae, Upper Triassic, are important time markers and apparently do not cross the Jurassic boundary (Kristan-Tollmann, 1960, 1966; Fuchs, 1970). The Oberhauserellidae, including the Triassic and Jurassic 'Globigerinas', may also be expected to become of greater biostratigraphic value with finer discrimination of the genera and species, as pioneered by Fuchs (1967, 1969, 1973). The Ceratobuliminacea are important from the Jurassic onwards, especially *Epistomina* (inc. *'Brotzenia'*) from the Middle Jurassic to the Albian (Cordey, 1963; Price, 1977; Shipp, 1978; Bartenstein, 1979).

With the rise of the buliminids and the rotaliids in the late Cretaceous the Robertinida become much less important in biostratigraphy. But they remain important at certain levels, i.e. *Ceratolamarckina* in the Palaeocene of the Gulf Coast, USA and N.W. Europe (Plummer, 1926; Brotzen, 1948) and *Alliatina,* a valuable index to the Pliocene in the North Sea area and the Mediterranean (Carter, 1957).

An attempt to achieve the finer biostratigraphical zonation possible through analysis of a lineage has been made by Copestake (1978) who has analysed *Reinholdella* and its allies in the Lower Lias of the Mochras Borehole. *Oberhauserella mesotriassica* which ranges into the highest Lower Lias is considered to be ancestor of the *Reinholdella* group. There appears to be two main lines of development. One through intermediate forms with open umbilicus and without toothplates, *Reinholdella? planiconvexa* (= *Oberhauserella planiconvexa* Fuchs). This species appears in the planorbis zone and is considered to have given rise to *R. dreheri* in the liassicus zone of the Hettangian and to *R. robusta* at the L./U. Sinemurian boundary. *R. dreheri* is considered to have given rise to *R. pachyderma* in the semicostatum zone and to *R. pachyderma humilis* in the raricostatum zone. The other line includes forms with open umbilicus but basal, 'chain-like' toothplates, *Reinholdella margarita. R. margarita dorsoplana* appears in the bucklandi zone and apparently gave rise almost immediately to *R.? mochrasensis. R. margarita margarita* appears in the turneri zone.

The importance of these reinholdellids in biostratigraphy is indicated by the zonation scheme erected for the Mochras Lias (figure 9.2). Five of the zone name index forams belong to this group and one subzone (not shown) is based on the first occurrence and acme of *R. pachyderma humilis* at the U. Sinemurian/L. Pliensbachian boundary.

ECOLOGY

At the present day the aragonitic group appears to be most abundant on the outer shelf and slope and many species of *Ceratobulimina, Robertina, Robertinoides* and *Hoeglundina* appear to be cosmopolitan (Brady, 1884; Cushman, 1923; Bandy, 1960a; Murray, 1973b). Low numbers relative to other orders of Foraminifera are probably an indication of their decline in the Cenozoic but must also be the result of the rapid dissolution of aragonite below 200 m. The organic membranes may hinder this process for a time, especially in deep basins with low oxygen levels.

A general preference for deep water in Recent representatives of the group has been taken to indicate a similar habitat for abundant aragonitic faunas in the mesozoic. Thus Brouwer (1969) regarded reinholdellids as indicating deepest, open-marine conditions in the Lias. On the other hand, Johnson (1976) in his detailed autecological study of the species in the Lias of the Mochras Borehole found that different species had different ranges:

R. macfadyeni, inner and midshelf.

R. dreheri, broadly tolerant, inner to outer shelf.

R. species, middle and outer shelf.

R. pachyderma, outermost middle and outer shelf.

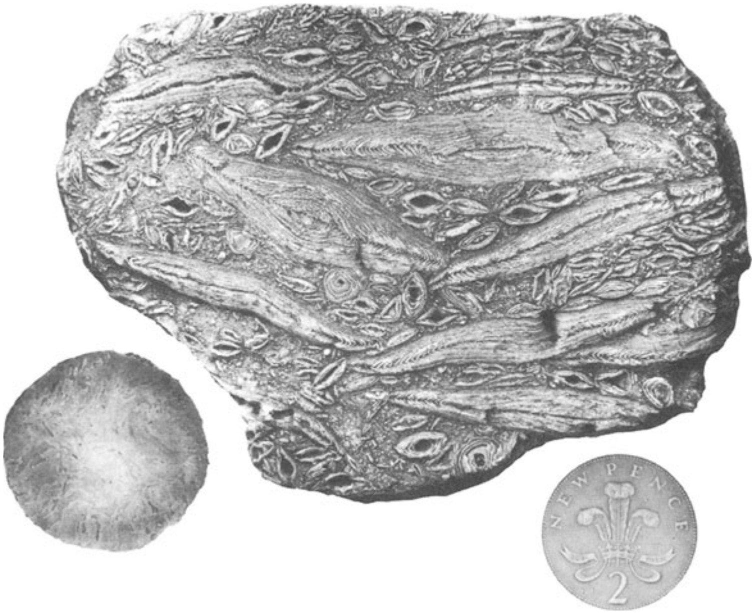
Although occurring across a broad range of depths these species reach their highest percentage occurrence (in the total foraminiferal fauna) in the environments interpreted as middle and outer shelf. They are particularly abundant in the lowermost Toarcian and at certain horizons reach total dominance. This facies is interpreted as poorly oxygenated, outer shelf.

The preferences of both the Buliminida and Robertinida for deep water, often poorly oxygenated, environments and the tendency to develop complicated internal structures may be related to the exploitation of particulate, detrital organic matter, discussed in chapter 10.

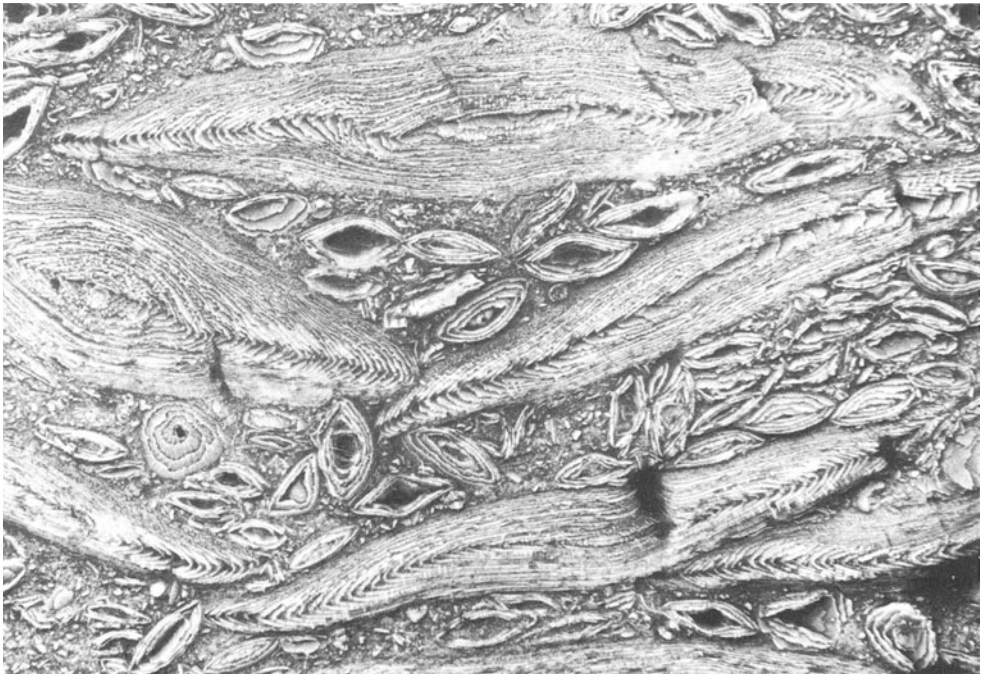
Although most of the early Mesozoic 'globigerinids' are now grouped with *Oberhauserella* their distinctive morphology and stratigraphical relationships suggested to Fuchs (1967) that they had become planktonic by the Rhaetic. Further work is clearly required on this interesting group.

Plates 1 to 15

PLATE 1

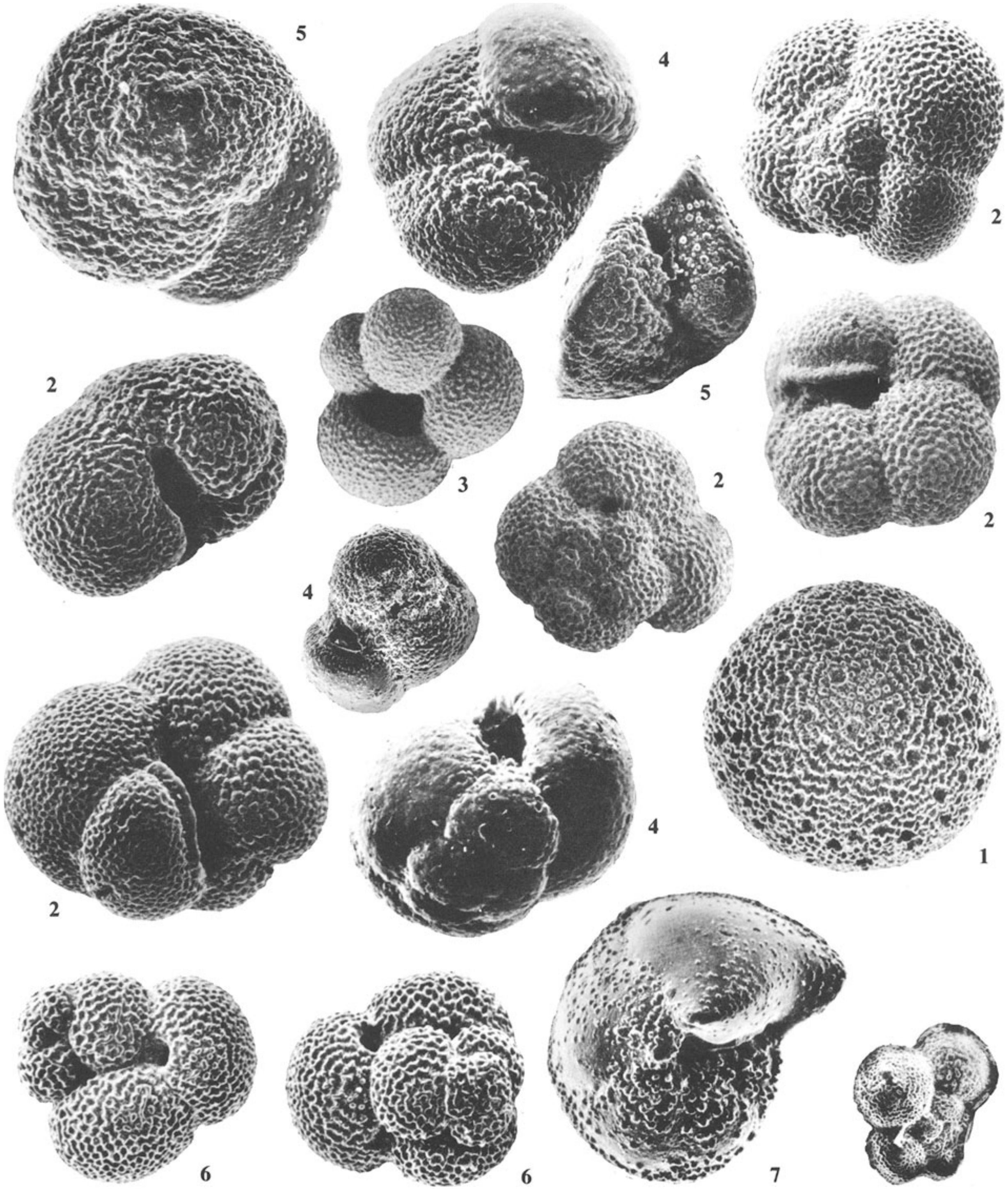


Hand specimen of nummulitic limestone from the Middle Eocene of the Western Desert, Libya, with left, a free specimen of *Nummulites gizehensis* showing traces of internal septa on the surface. Approx. seven tenths natural size



Close up of hand specimen, showing the two generations of *N. gizehensis*: large, asexual, B forms with many whorls and chambers (microspheric); small, sexual, A forms with relatively few whorls and chambers (megalospheric). The large proloculus can be seen in a number of the A forms. Almost one and a half times natural size

PLATE 2A



Temperate latitude, 'transitional province', planktonic Foraminifera. Quaternary, N.E. Atlantic (photography by SEM; magnifications between × 35 and × 75)

1 *Orbulina universa;* 2 *Turborotalia pachyderma;* 3 *Globigerina bulloides;* 4 *Turborotalia inflata;* 5 *Globorotalia crassaformis;* 6 *Globigerinoides ruber;* 7 *Globorotalia truncatulinoides;* 8 *Biorbulina bilobata*

Plate 2A *(continued)*

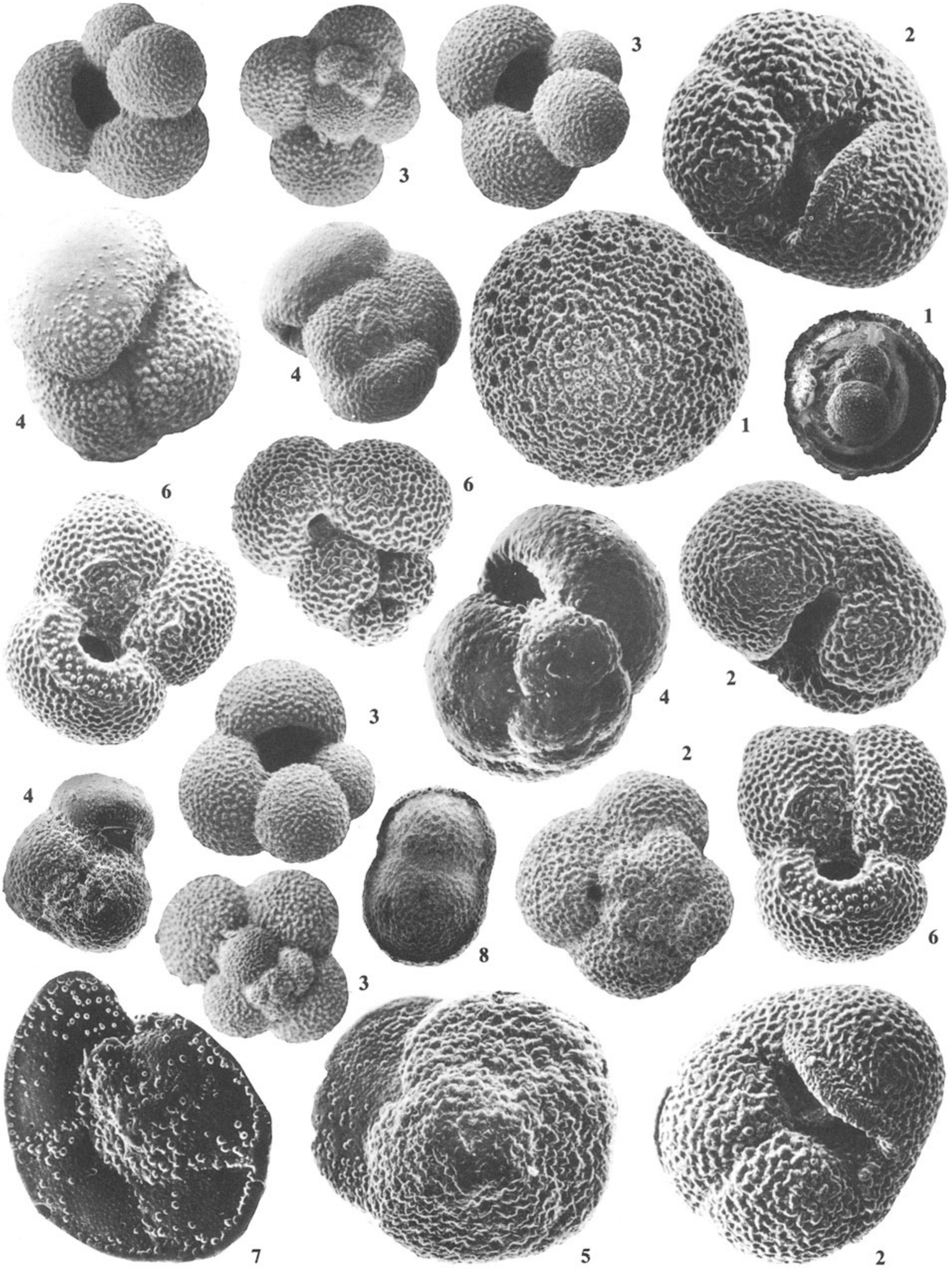
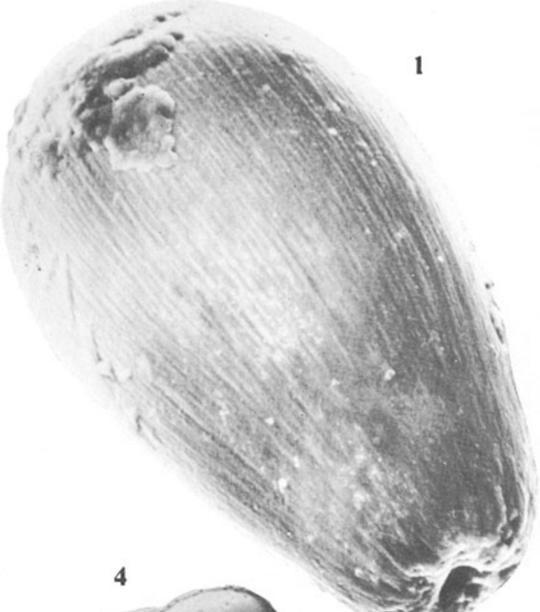


PLATE 2B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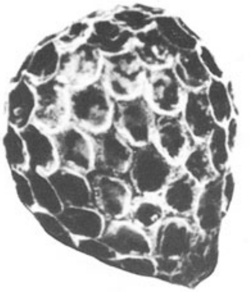
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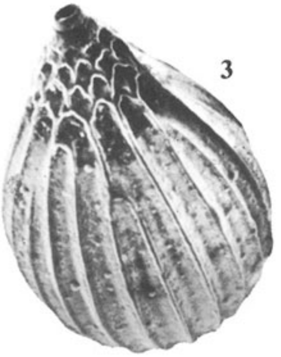
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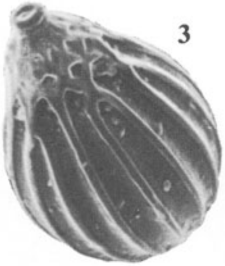
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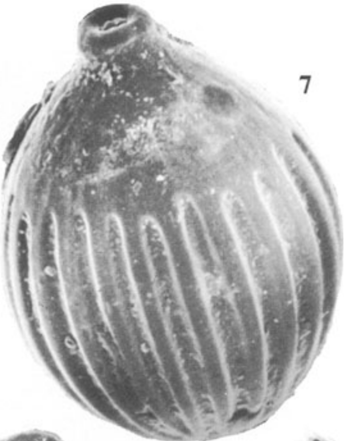
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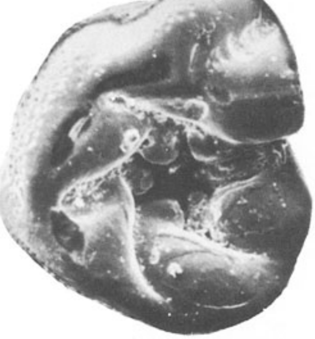
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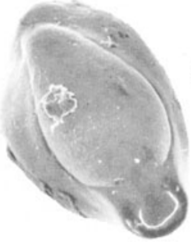
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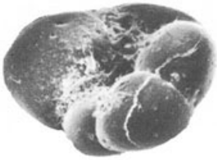
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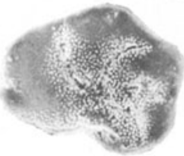
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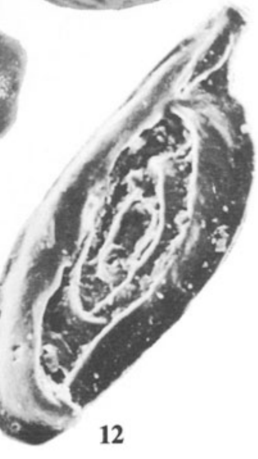
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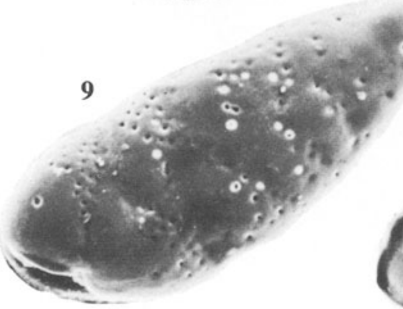
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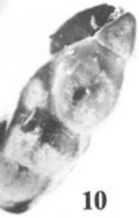
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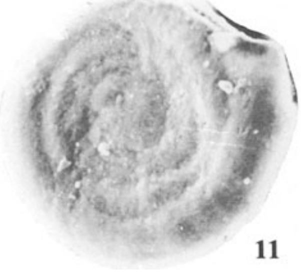
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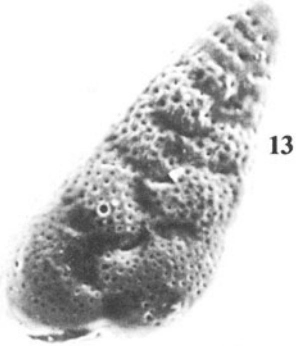
Temperate latitude benthonic Foraminifera. Quaternary, N.E. Atlantic, shelf assemblage (photography by SEM)

1 ***Oolina lineata,*** **× 450; 2** ***Oolina hexagona,*** **× 135; 3** ***Oolina williamsoni,*** **× 135; 4** ***Rosalina anomala,*** **× 50; 5** ***Trochammina inflata,*** **× 50; 6** ***Pyrgo*** **sp., × 80; 7** ***Oolina borealis,*** **× 135; 8** ***Elphidium magellanicum,*** **× 95; 9** ***Bolivina (Brizalina)*** **cf.** ***vadescens,*** **× 135; 10** ***Bulimina elongata lesleyae,*** **× 80; 11** ***Cornuspira selseyensis,*** **× 135; 12** ***Spirophthalmidium acuta emaciata,*** **× 135; 13** ***Bolivina variabilis,*** **× 135; 14** ***Rosalina*** **cf.** ***bradyi,*** **× 135; 15** ***Asterigerinata mamilla,*** **× 135 and × 95; 16** ***Elphidium williamsoni,*** **× 135; 17** ***Turrispirillina*** **sp., × 95; 18** ***Rosalina neapolitana,*** **× 225; 19** ***Rosalina*** **sp., × 80; 20** ***Bolivina (Brizalina) striatula,*** **× 135; 21** ***Oolina laevigata,*** **× 115; 22** ***Haynesina depressulum,*** **× 95; 23** ***Trifarina angulosa fluens,*** **× 135; 24** ***Trochammina astrifica,*** **× 135; 25** ***'Stainforthia' fusiformis,*** **× 135;**

Plate 2B *(continued)*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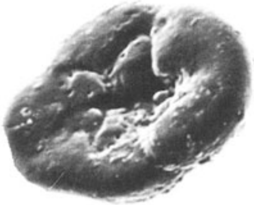
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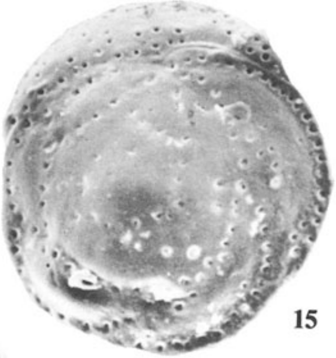
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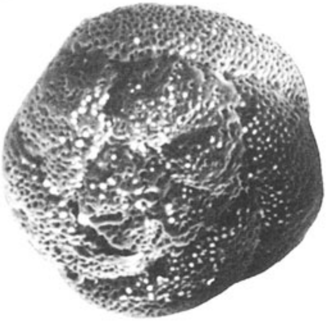
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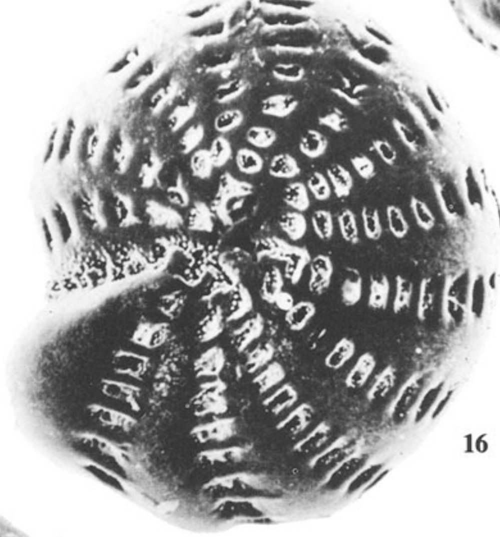
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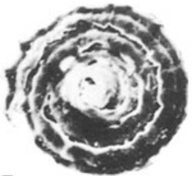
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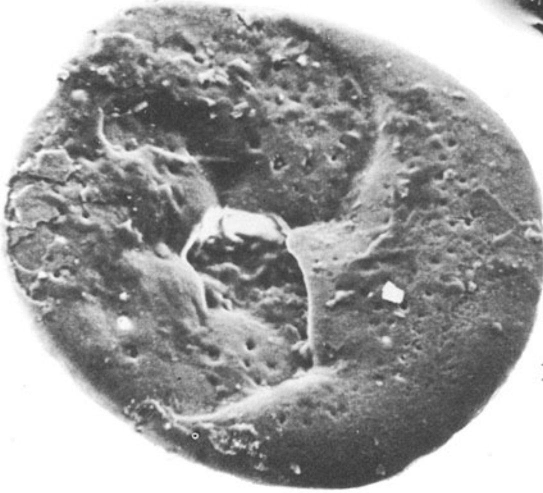
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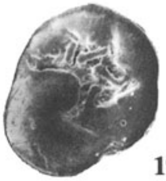
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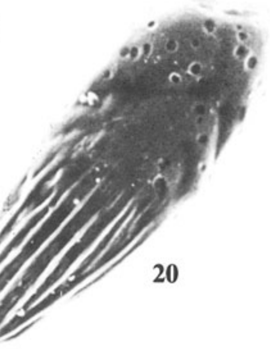
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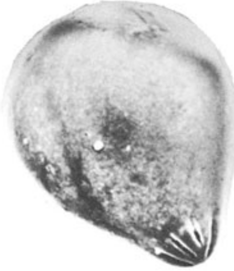
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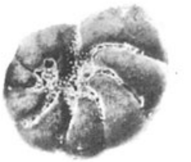
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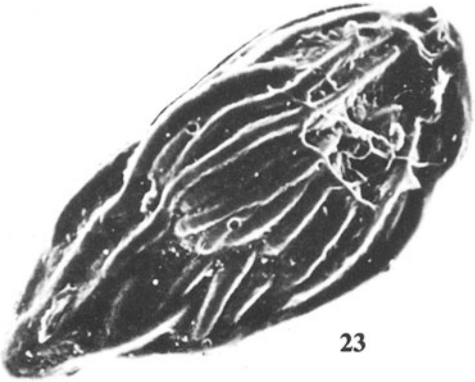
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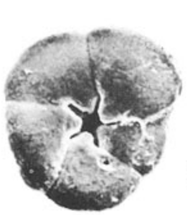
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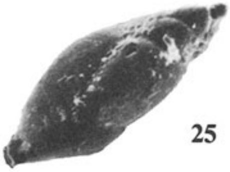
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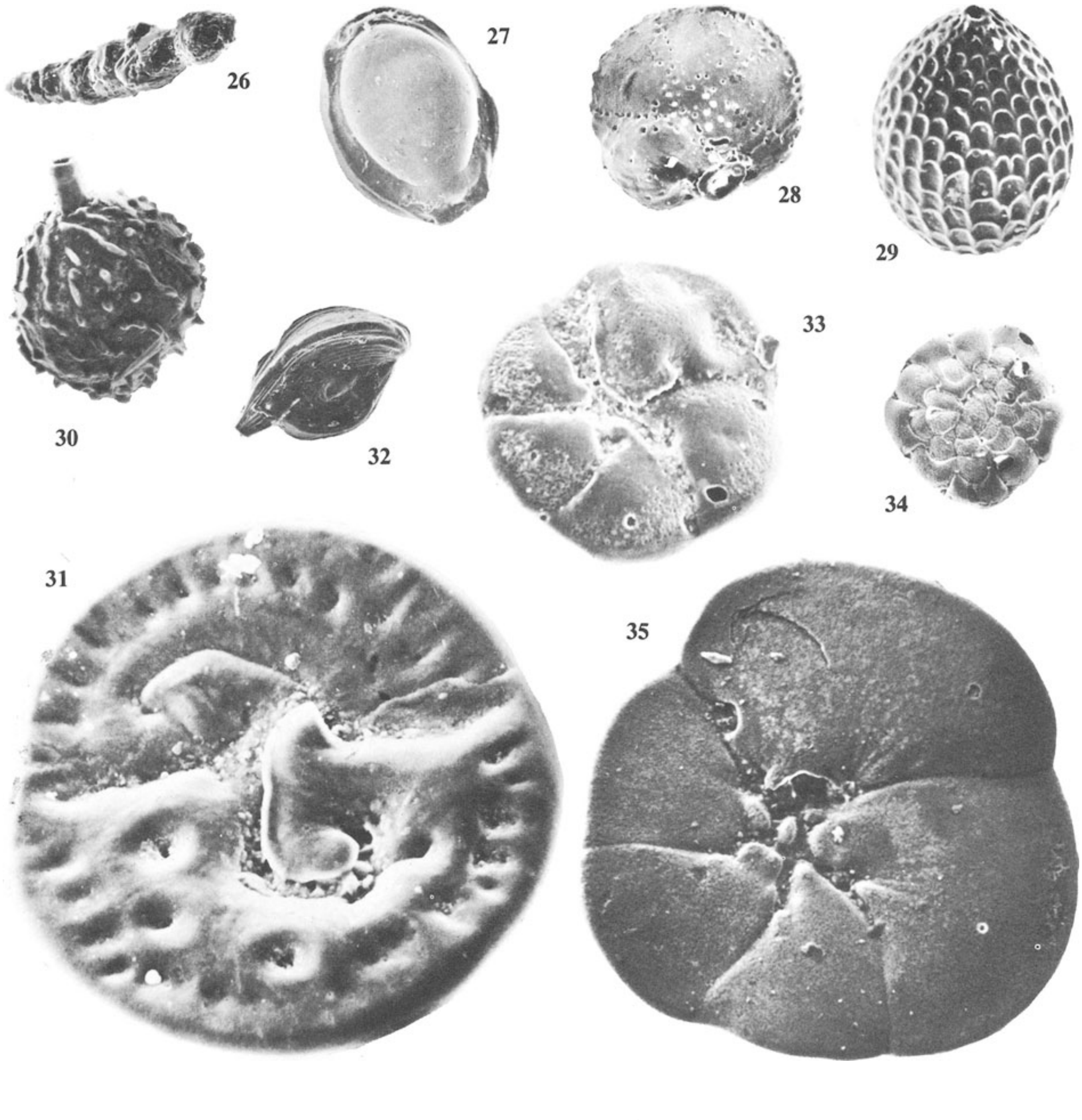
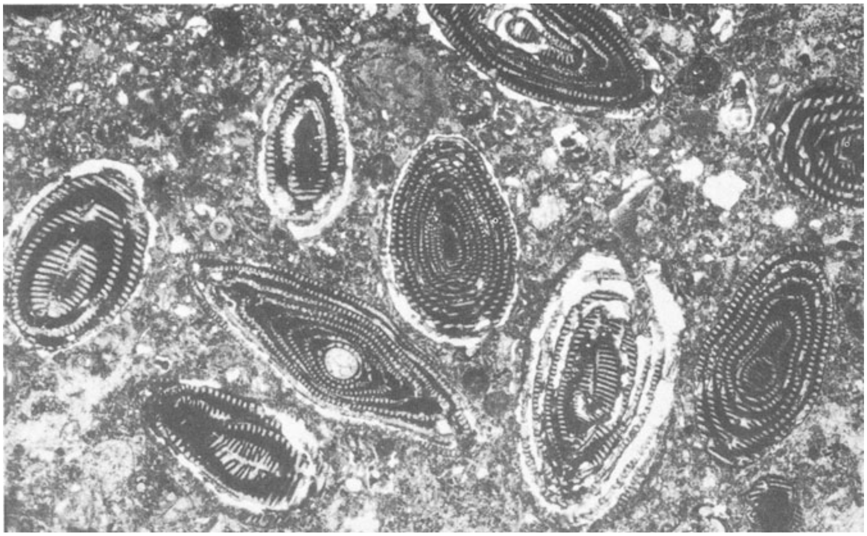
(continued overleaf)

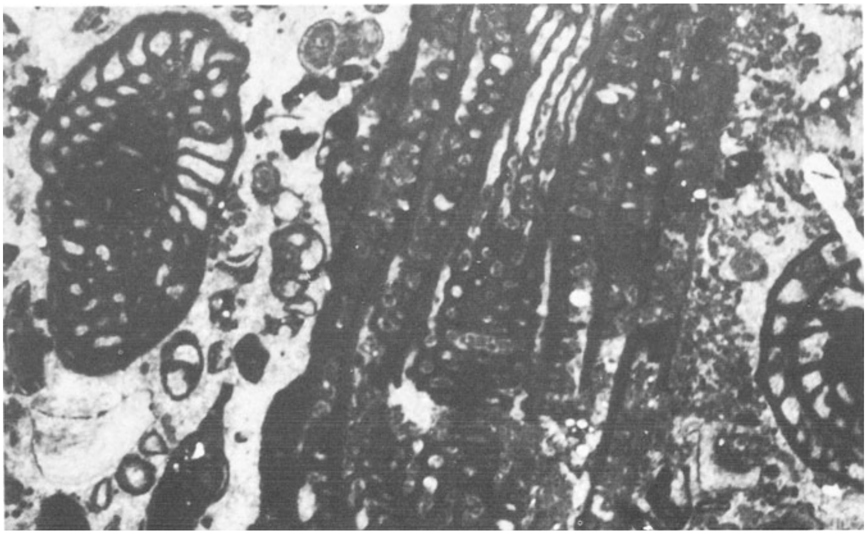
Plate 2B *(continued)*



26 *Reophax arcticus,* × 125; **27** *Pyrgo* cf. *constricta,* × 45; **28** *Siphonina georgiana,* × 95; **29** *Oolina squamosa,* × 135; **30** *Lagena hibernica,* × 250; **31** *Patellina corrugata,* × 375; **32** *Quinqueloculina mediterranensis,* × 45; **33** *Gavelinopsis praegeri,* × 160; **34** *Planorbulina distoma,* × 50; **35** *Rosalina williamsoni,* × 170

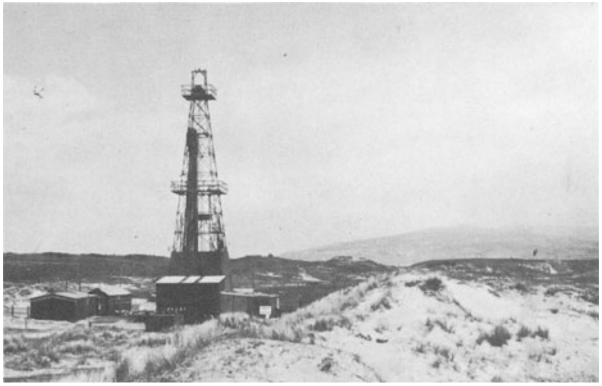


Fine-grained shelly, foraminiferal limestone with *Alveolina ex. gr. ovoidea* seen in axial and oblique axial sections. Note single row of chamberlets in each chamber, produced by insertion of spiral septula, and thick deposits of secondary calcite on the chamber floors (flosculin), showing as a dark infilling. From the L. Eocene of Sirtica, Libya. Photomicrograph by ordinary light, × 10



Fusuline limestone with very large specimens of *Schwagerina* sp. in a clear calcite groundmass with smaller Foraminifera and shell fragments. Portion of axial section centre, showing thickened 'schwagerinid' wall and intense septal folding which has produced oval chamberlets. Portion of median section far right. From the Permian of New Mexico (Capitan Limestone). Photomicrograph by ordinary light, × 16

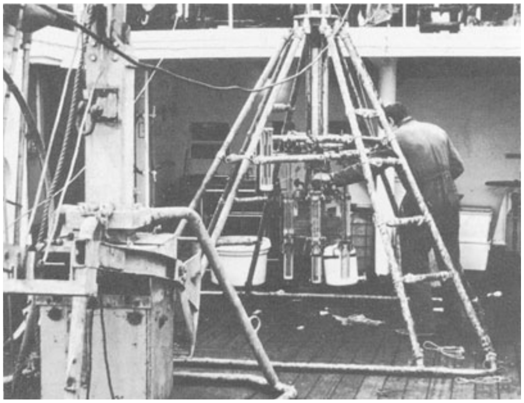
PLATE 4



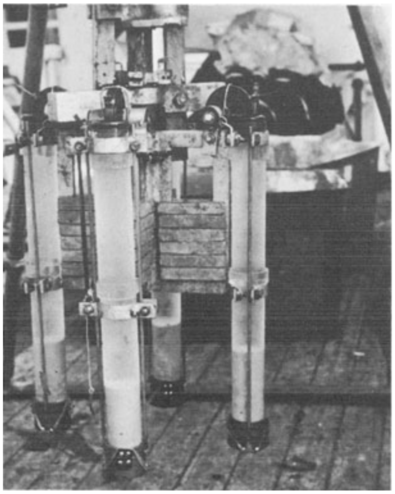
1 The drilling rig on Mochras Island which proved Tertiary and Mesozoic rocks in subsurface Cardigan Bay (Wales)

2 Extracting core at Mochras

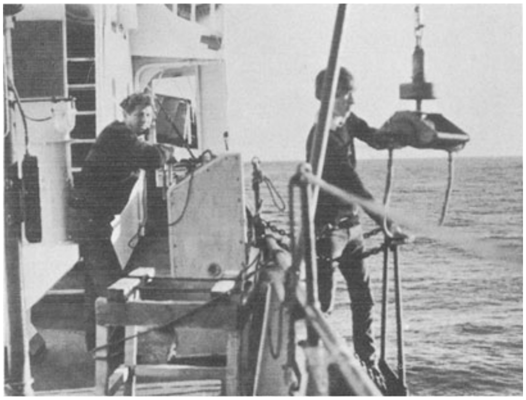
3 Geologists examining Liassic core at Mochras (Prof. A. Wood and Dr D. Bates)



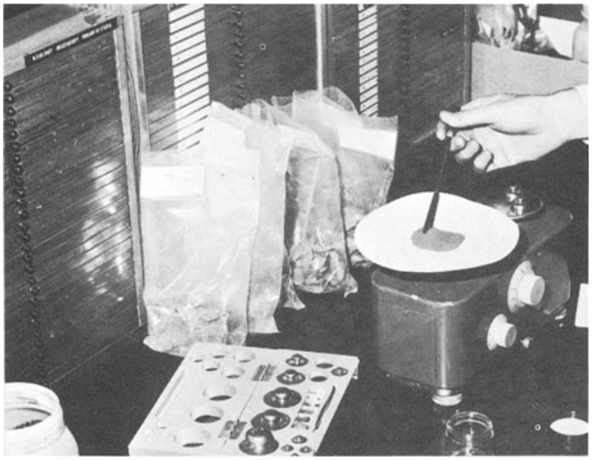
4 The Barnett and Watson Multiple Corer being prepared for use on the deck of R.V. 'Challenger'



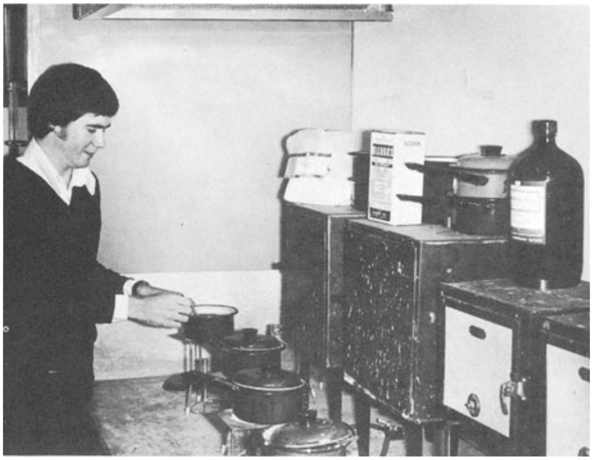
5 The Multiple Corer after retrieval from the floor of Rockall Trough, N. Atlantic (over 2000 fathoms depth), showing undisturbed cores of *Globigerina* Ooze



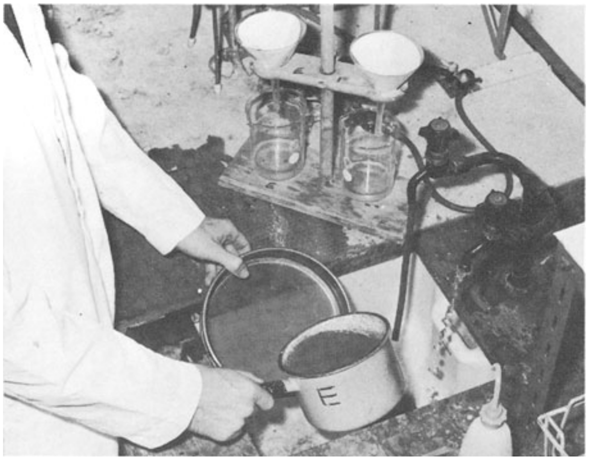
6 Shipek Grab on board R.V. 'John Murray' cocked for sampling the sediments of St. George's Channel



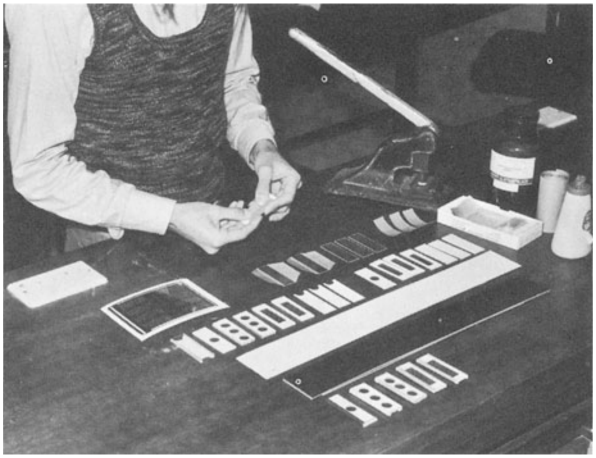
1 **Weighing out crushed sample prior to washing**



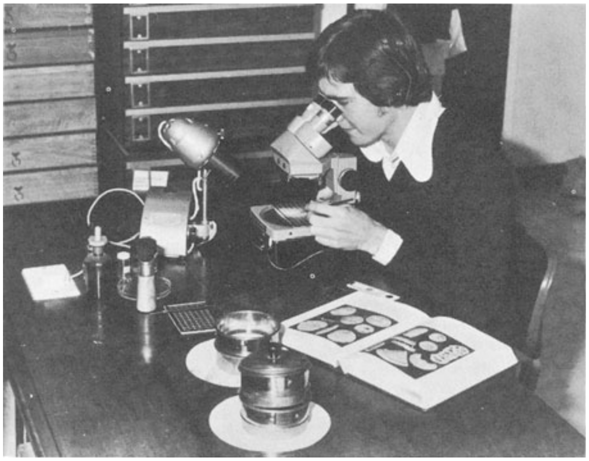
2 **Simple boiling beneath canopy**



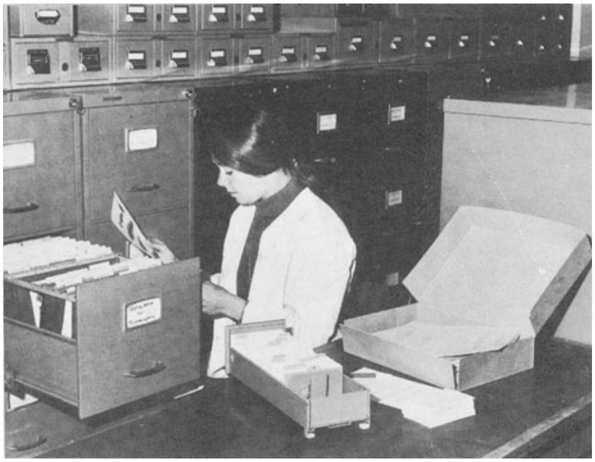
3 **Decanting through fine-mesh sieve**



4 **Making 'one-hole', 'three-hole' and faunal grid slides**



5 **Picking microfauna from washed residue on a gridded tray**

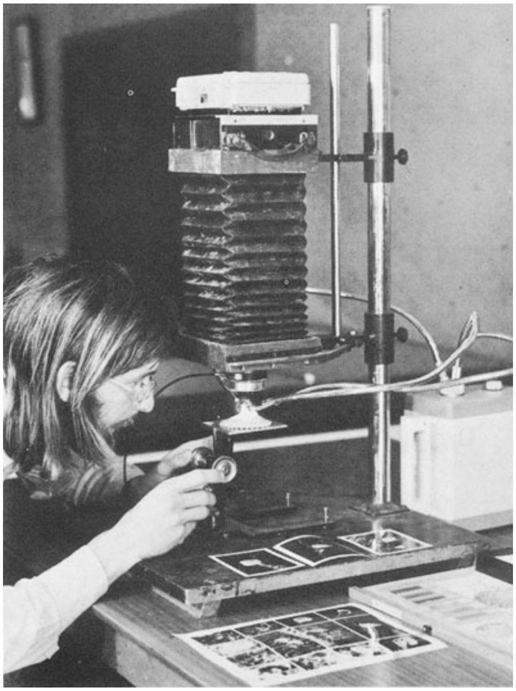


6 **Consulting the 'Ellis and Messina' Foraminiferal Catalogue and 'separates' of other literature**

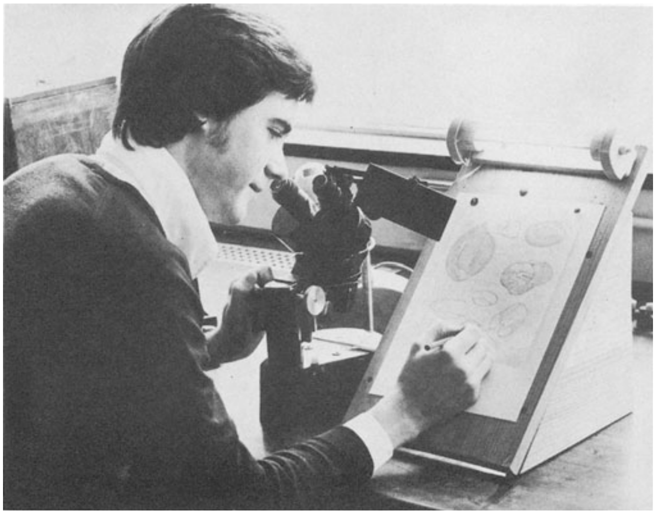
1 Operating the scanning electron microscope

2 Assembling SEM photographs on black card

3 Photographing small Foraminifera attached to a bivalve shell

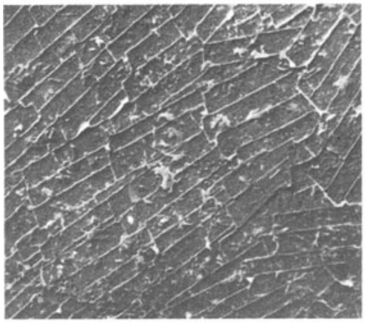


4 Drawing specimens. Note 'camera lucida' attachment to the binocular microscope



Wall structure

PLATE 7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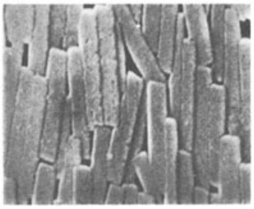
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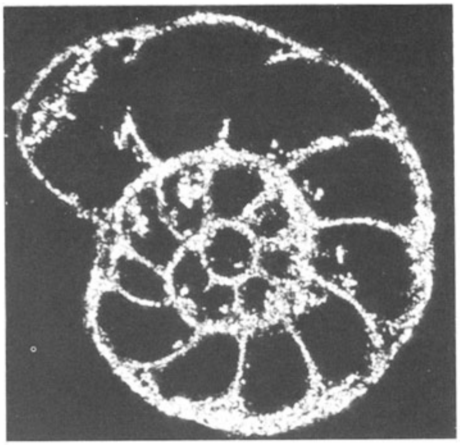
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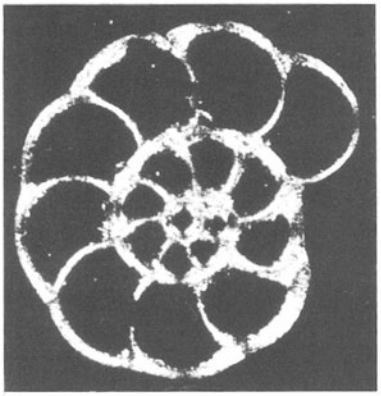
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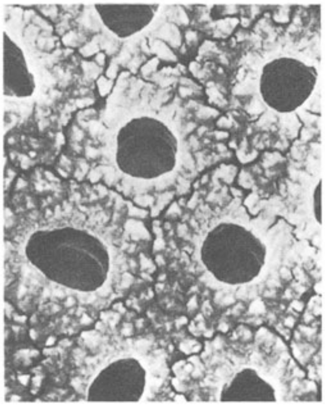
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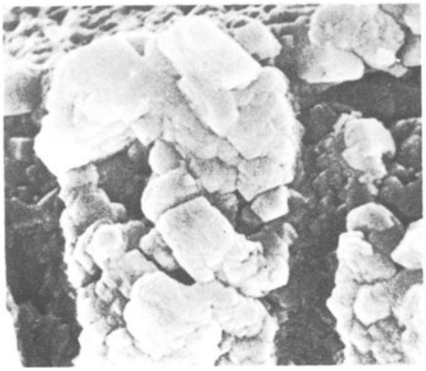
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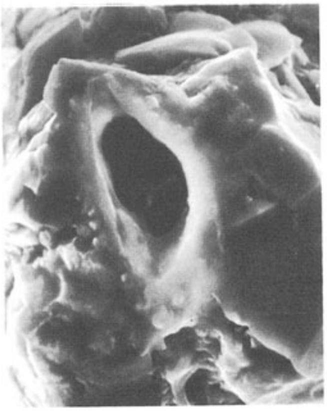
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1 Neat mosaic of calcite laths in the external layer of the porcelaneous species, *Quinqueloculina seminulum,* × 7000, by TEM. From Towe and Cifelli (1967)

2 Similarly arranged calcite laths in the external layer of *Triloculina tricarinata,* × 7000, by SEM. From Haake (1971)

3 Oblique hyaline structure in *Elphidium exoticum,* ×210, under crossed nicols. Note 'granular' appearance

4 Radial hyaline structure in *Elphidium selseyense,* × 112, under crossed nicols. Note extinction cross in proloculus and shadows across other chambers

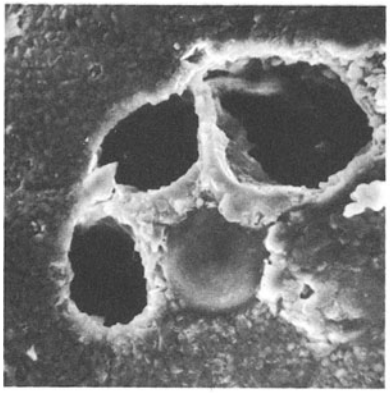
5 Pores piercing sutured units of microcrystals in the radial hyaline species *Ammonia batava,* × 7000, by SEM after etching. From Bellemo (1974a)

6 Stacks of rhomboid microcrystals in *Ammonia batava,* with pores seen in section, × 7000, by SEM after etching. From Bellemo (1974a)

7 Aperture in *Reophax arcticus,* showing abundant cement, × 1050, by SEM

(continued overleaf)

Plate 7 ***(continued)***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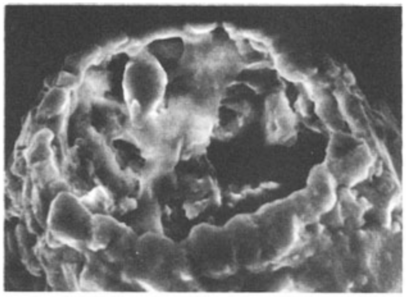
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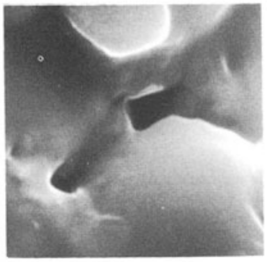
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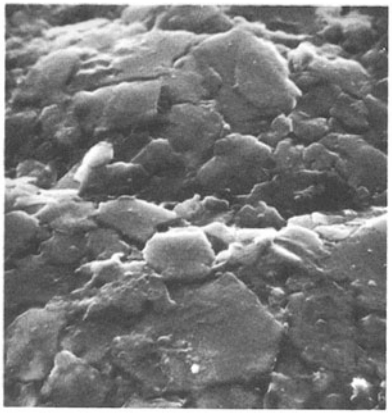
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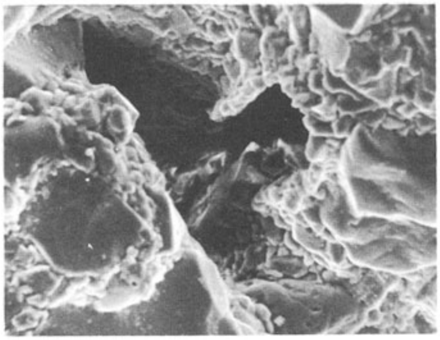
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8 **Detail of breached dorsal side of *Trochammina inflata* showing minute agglutinated grains and tectin lining, × 490, by SEM**

9 **Fine structure of the apertural lip in the agglutinating species *Lagenammina arenulata*, showing size selection, × 735, by SEM**

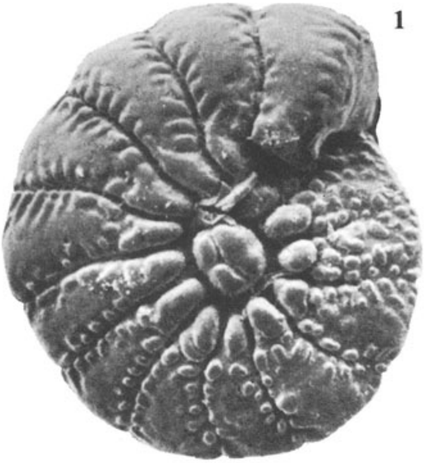
10 **Small, rectangular pores in the agglutinated species *Reophax arcticus*, × 4900, by SEM**

11 **Irregular grains arranged flat-on in the agglutinated species *Trochammina intermedia?*, × 1050, by SEM**

12 **Detail of the apertural tooth in the agglutinating species *Eggerelloides scaber*, showing size selection. Note also how the large grains in the wall are packed in a matrix of small grains, × 350, by SEM**

PLATE 8

1



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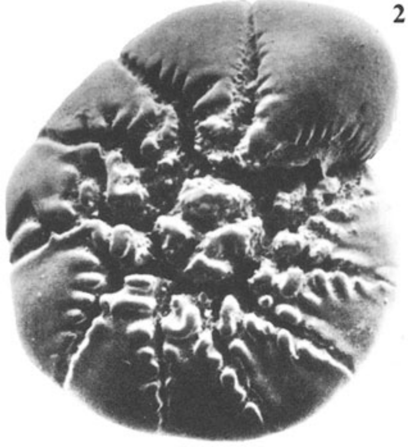

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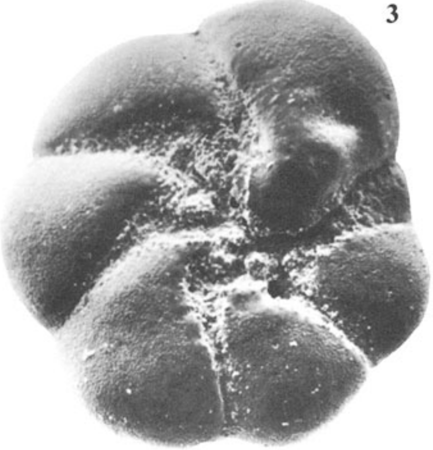

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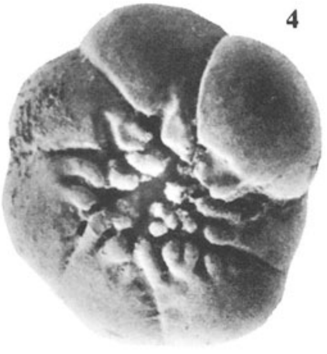

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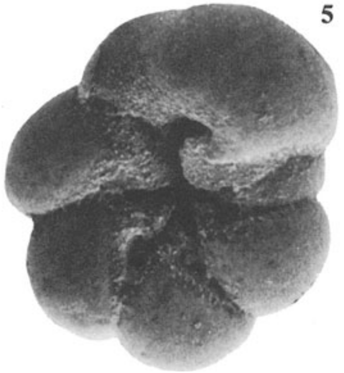

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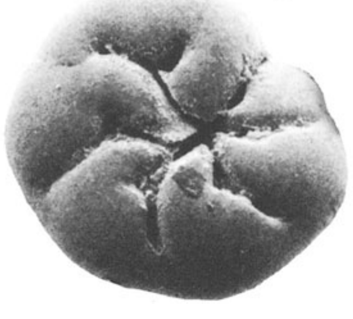

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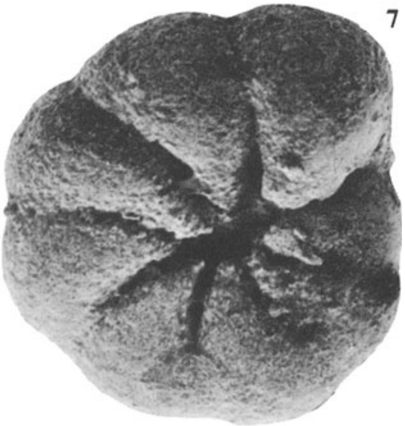
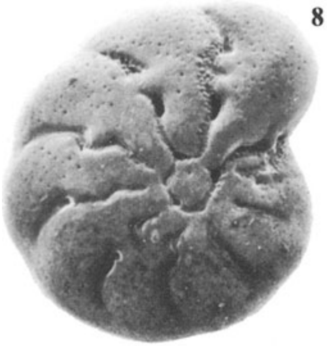


(all photography by SEM)

1–7 *Ammonia ex gr. beccarii* (Linné)
  1 *A. beccarii* s.s. topotype from the Adriatic, × 60
  2 *A. batava* (Hofker), Recent, Lough Swilly, Ireland, × 75
  3 *A. tepida* (Cushman), Recent, Lough Swilly, Ireland, × 75
  4 *A.* species A., Ipswichian, Burtle Beds, Somerset, × 75
  5 *A. flevensis* (Hofker), Ipswichian, Burtle Beds, Somerset, × 160
  6 *A. limnetes* (Todd & Brönnimann), Ipswichian, Burtle Beds, Somerset, × 160
  7 *A. aberdoveyensis* Haynes, Ipswichian, Burtle Beds, Somerset, × 160

(continued overleaf)

Plate 8 *(continued)*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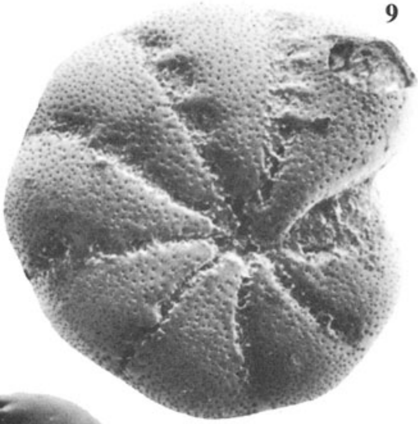
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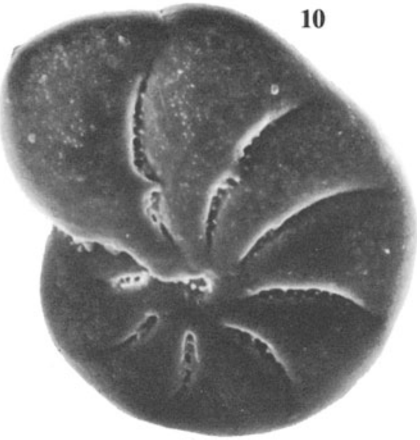
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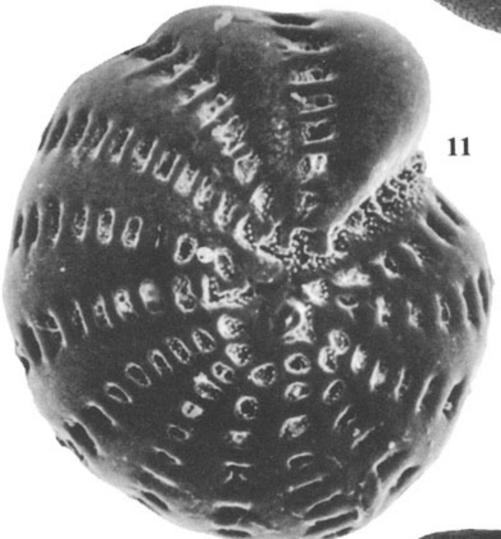
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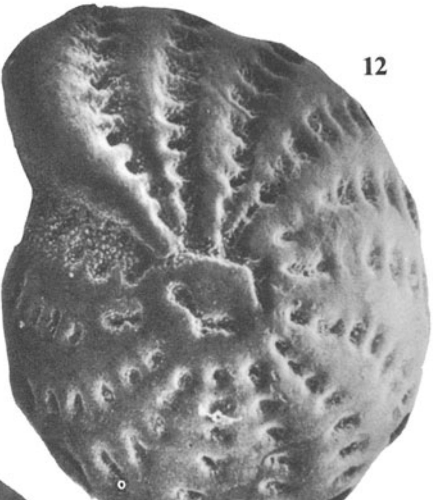
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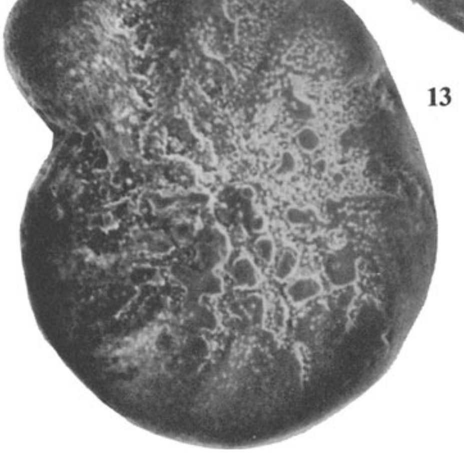
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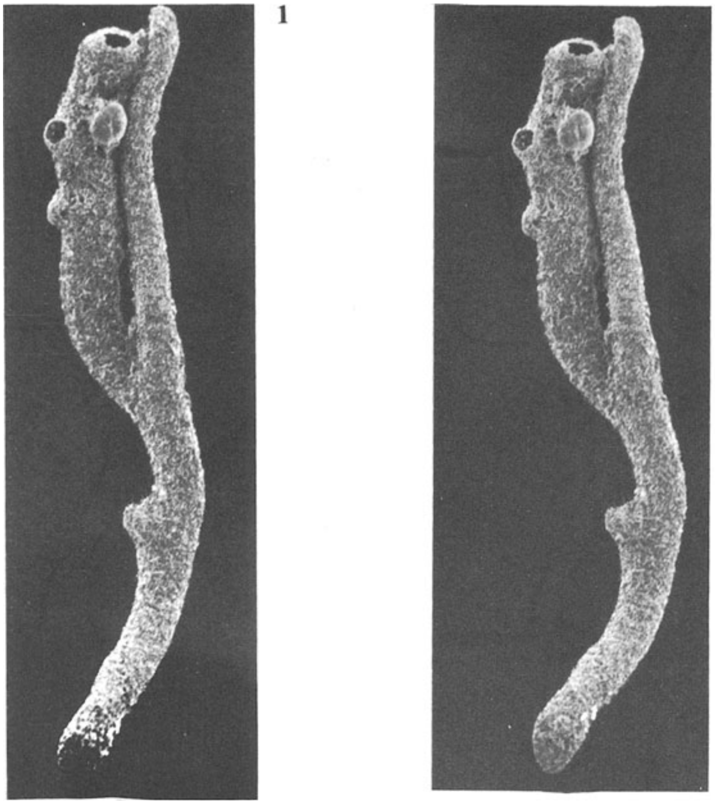
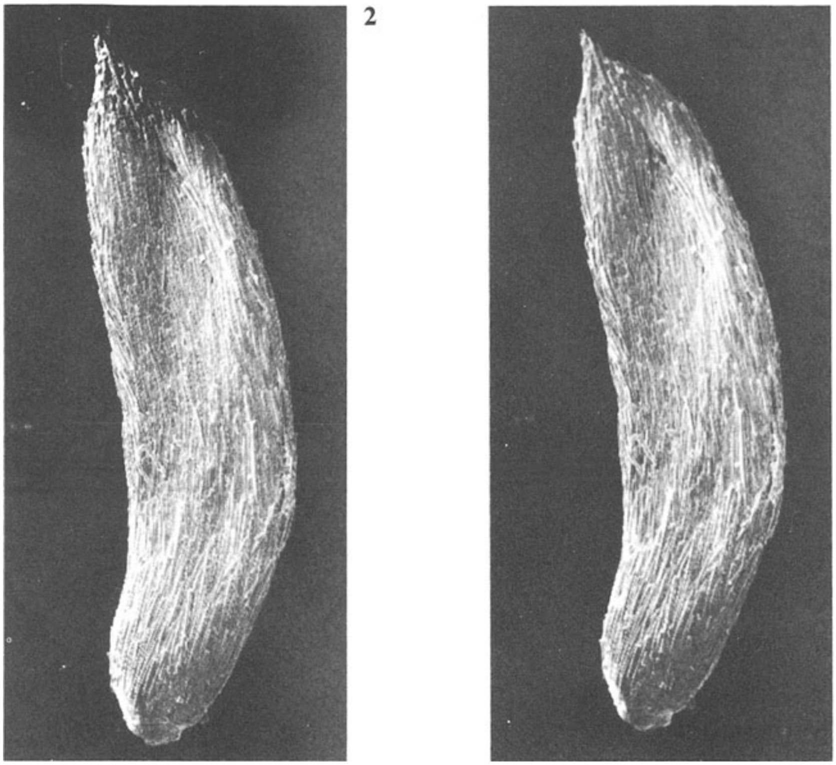
8 – 13 *Elphidium ex. gr. excavatum* (Terquem)
- 8 *E. clavatum* (Cushman), Pleistocene, Isle of Man, × 100
- 9 *E. excavatum* (Terquem) s.s., Ipswichian, Selsey, Sussex, × 140
- 10 *E. incertum* (Williamson), Recent, Dovey Estuary, Wales, × 375
- 11 *E. williamsoni* Haynes, Recent, Dovey Estuary, Wales, × 135
- 12 *E.* cf. *advenum,* sensu Todd & Low, Ipswichian, Burtle Beds, Somerset, × 120
- 13 *E. selseyense* (Heron-Allan & Earland), Recent, Cardigan Bay, Wales, × 150

Comparison between sponges and spicular agglutinated species PLATE 9



1:1 Stereopair showing branching sponge, *?Clathrina* sp. (note small, attached foram), × 20



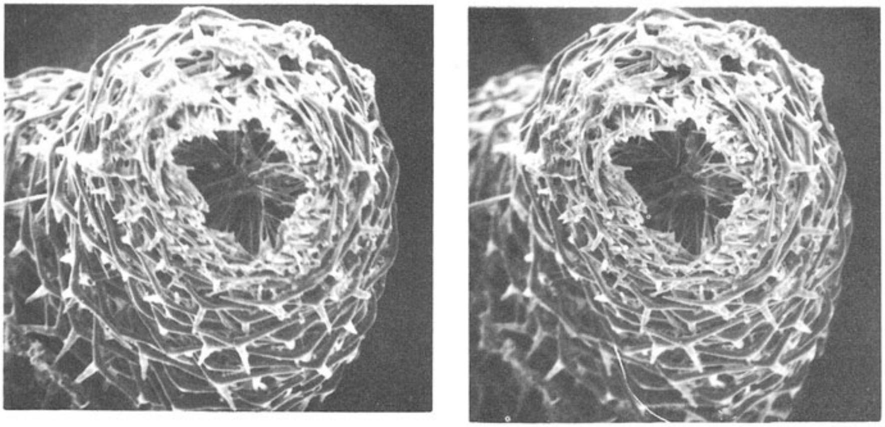
2:2 Stereopair of *Technitella legumen*, × 45. Brady material, Isle of Man

(all photography by SEM; 1:1, 2:2, 3:3, 5 and 7 courtesy of Dr J.E. Whittaker, B.M., Nat. Hist.)

(continued overleaf)

Plate 9 *(continued)*

3 3



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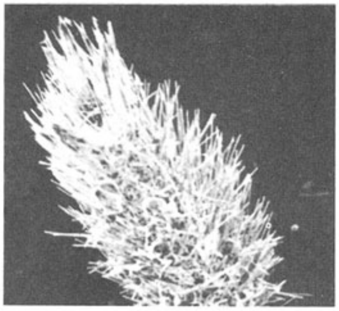

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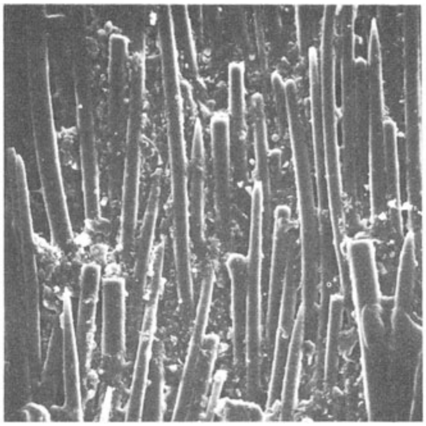

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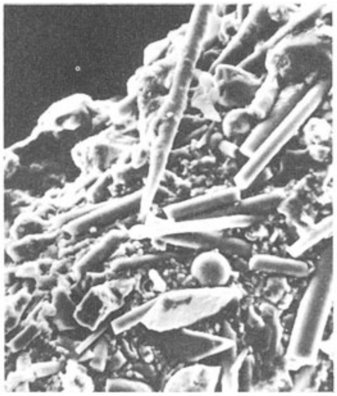

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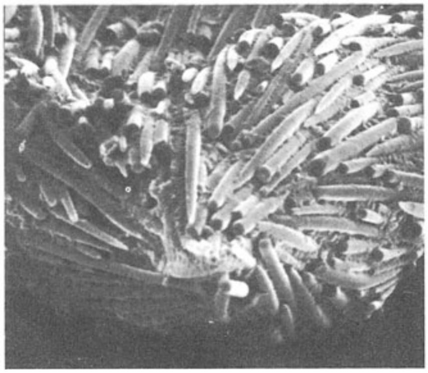


3:3 Stereopair of aperture in *?Clathrina* sp., showing triradiate spicules arranged like the needles in a pin-cushion and criss-crossing the interior, × 122

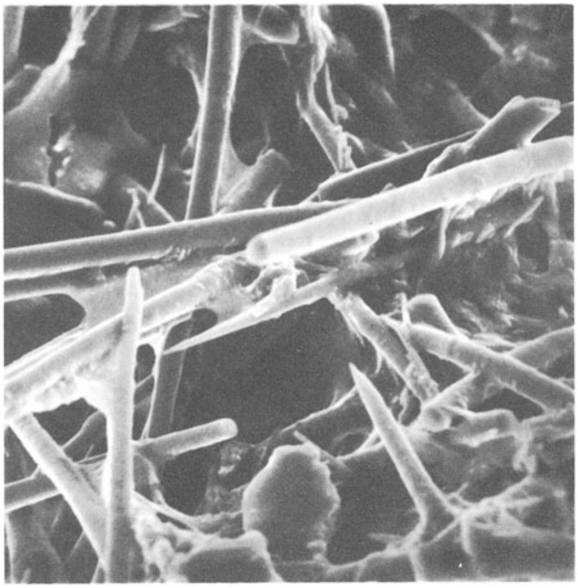
4 Side view of paratype of *Technitella teivyensis,* showing monaxon spicules brushed forward around the aperture, × 48

5 Close-up of tylostyles in *T. legumen,* some with the knob ends directed outwards, × 250

6 Detail of spicular wall structure in the agglutinating species *Halyphysema tumanowiczii,* × 210

7 Apertural end of *T. legumen,* × 200

8



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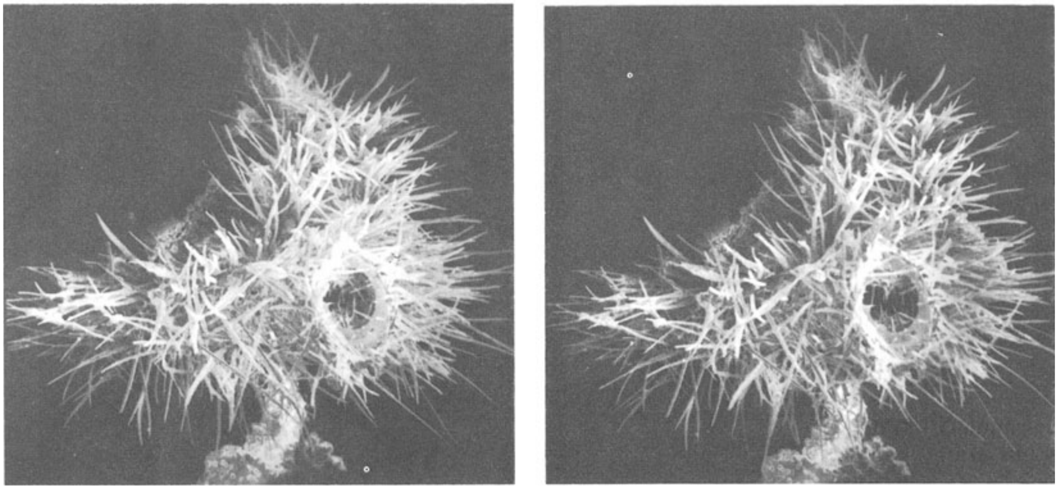
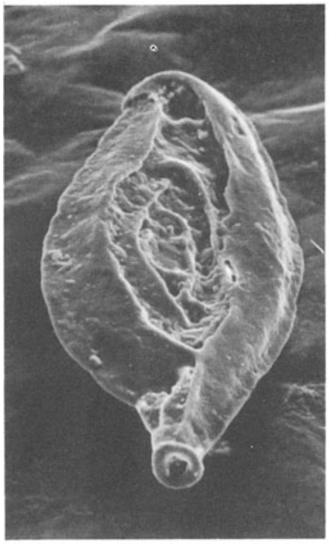


8 Detail of wall structure in *T. teivyensis,* × 880

9:9 Stereopair showing apertural view in *T. teivyensis* (note how the monaxons criss-cross the interior, as in *?Clathrina* sp., nos. 3:3. However, this is also shown by the agglutinating, spicular genus *Botellina*), × 65

PLATE 10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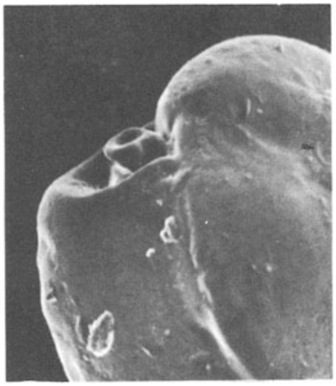
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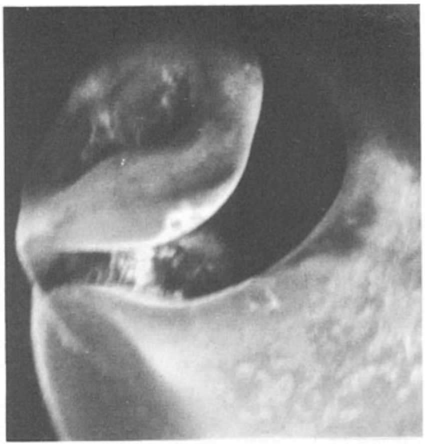
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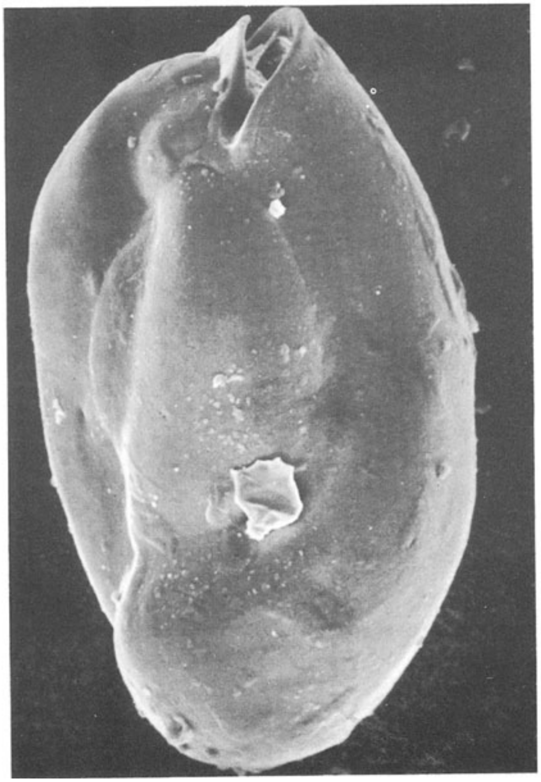
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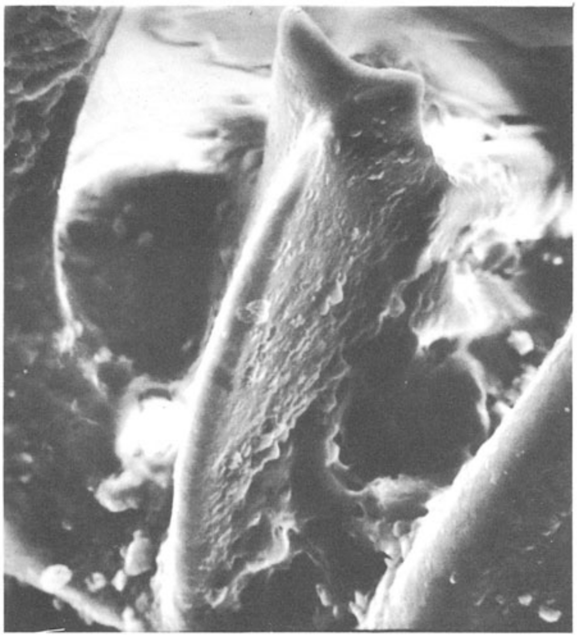
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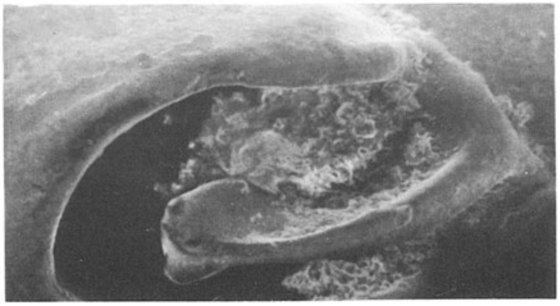
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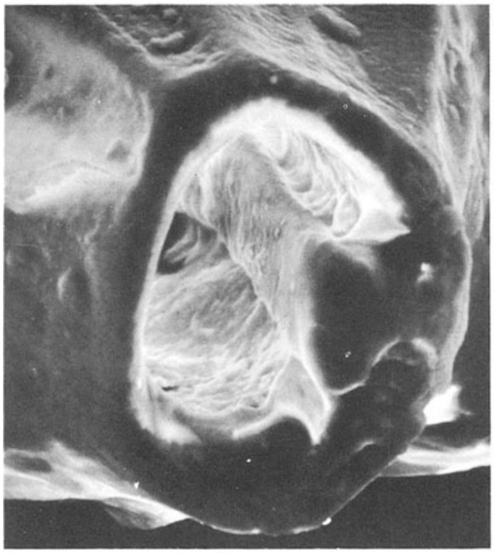
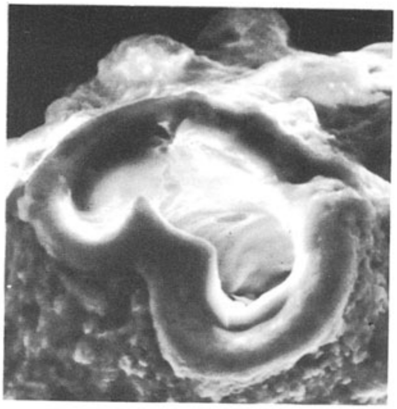
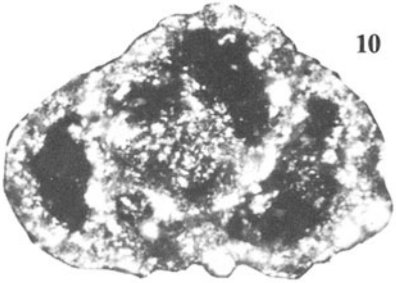
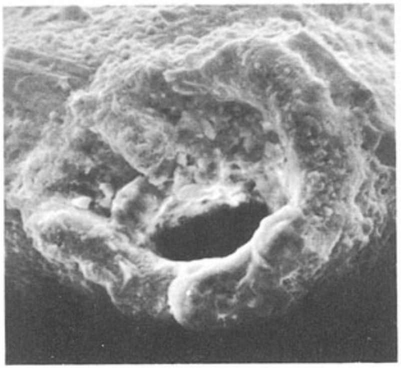
(aperture form by SEM and chamber arrangement by light photomicrographs in some miliolids)

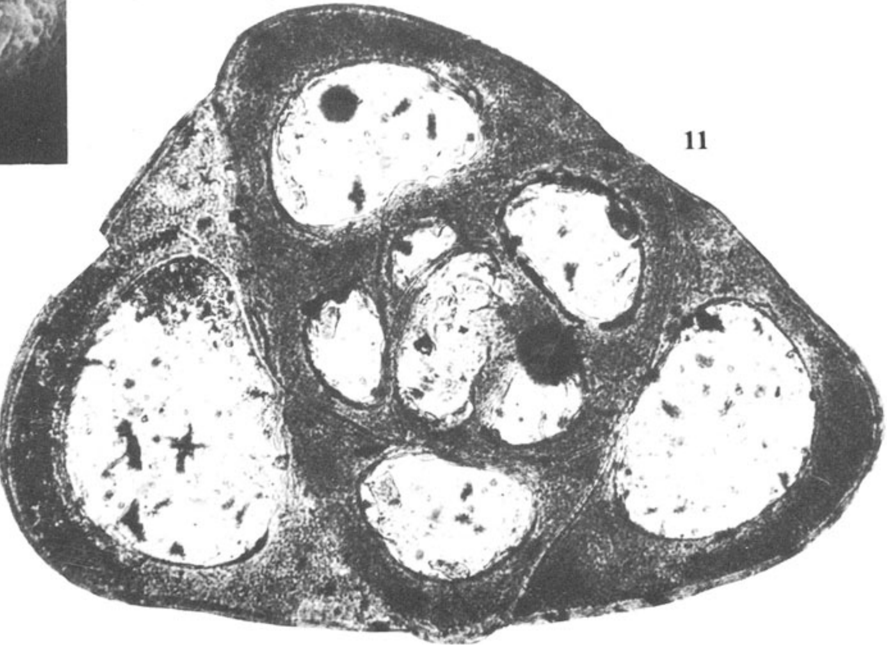
1 *Spirophthalmidium emaciatum,* oblique view of simple aperture, × 220
2 *Triloculina* sp., spoon-shaped tooth, × 100
3 *Miliolinella oblonga,* flap-like tooth, × 160
4 *Scutuloris* sp., side view of flap-like tooth, × 220
5 *Quinqueloculina seminulum,* bar-like tooth with bifid end, × 925
6 *Massilina secans* var., bar-like tooth with bifid end, × 160







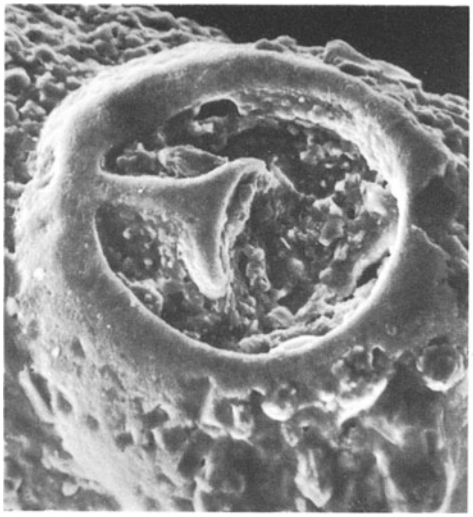




- 7 *Adelosina mediterranensis,* **produced neck and wedge-like tooth, × 460**
- 8 *Sigmoilopsis moyi,* **short, wedge-like tooth, × 1150**
- 9 *Miliammina fusca,* **elongate, wedge-like tooth, × 460**
- 10 *Miliammina fusca,* **horizontal section by crossed nicols to show agglutinated grains, × 210**
- 11 *Quinqueloculina seminulum,* **horizontal section by ordinary light showing tripartite structure, × 320**

(continued overleaf)

Plate 10 *(continued)*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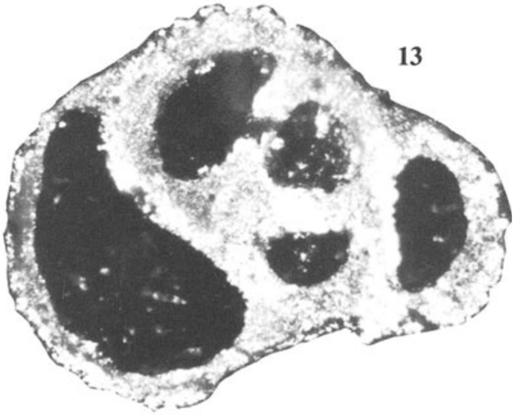
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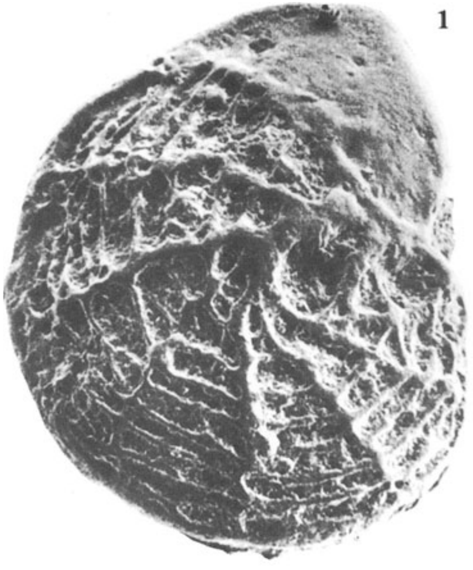
12 *'Adelosina' aspera,* round aperture with wedge-like tooth with thin stem, × 460

13 *'Adelosina' aspera,* horizontal section by crossed nicols to show partly agglutinated wall, × 160

Characteristic nodosariids from the Mochras Lias, N. Wales **PLATE 11**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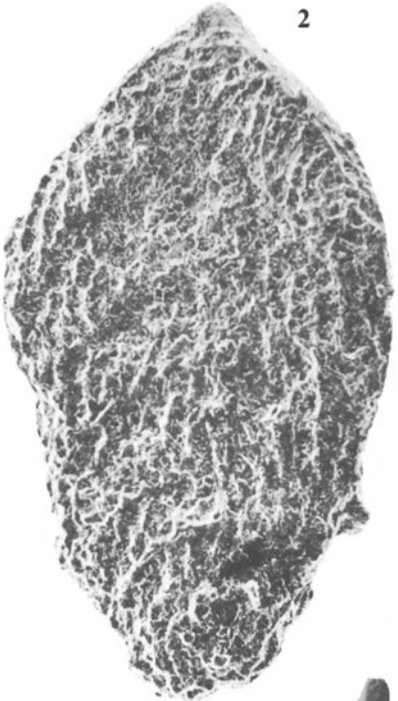
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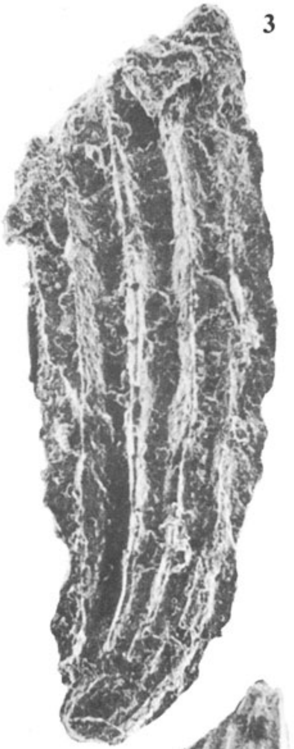
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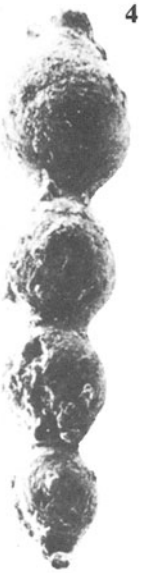
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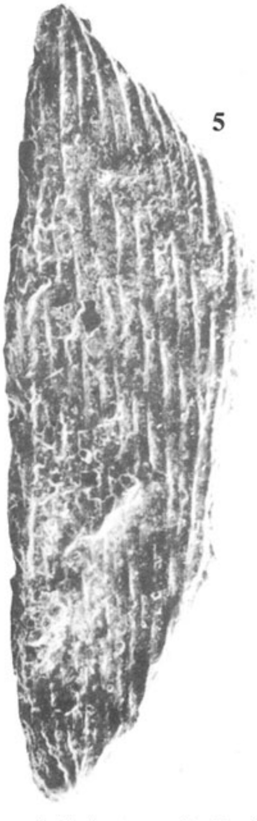
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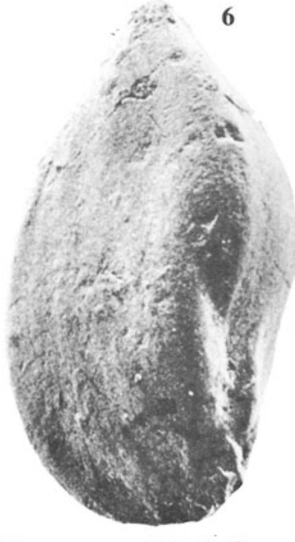
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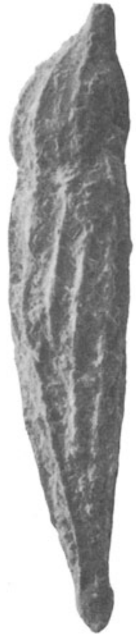
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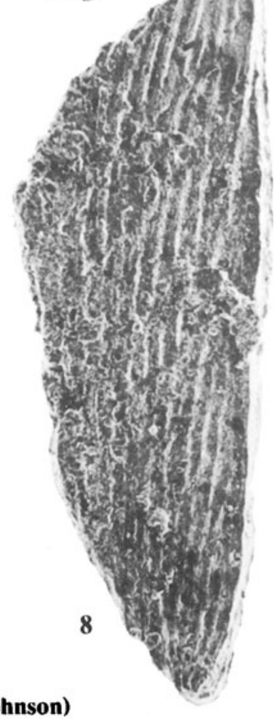
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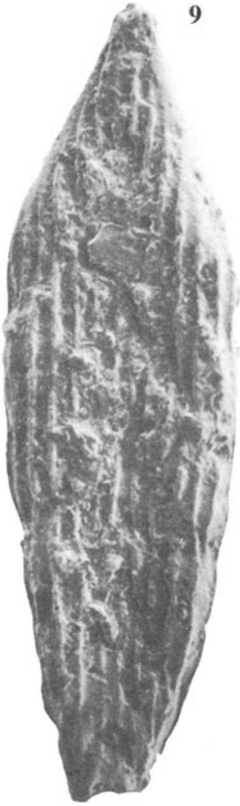
(all photography by SEM, courtesy of Dr P. Copestake and Dr B. Johnson)

1 ***Lenticulina dorbignyi*, side view, × 200**
2 ***Palmula tenuicostata*, side view, × 300**
3 ***Vaginulina proxima*, side view, × 200**
4 ***Nodosaria regularis robusta*, side view, × 200**
5/8 ***Citharina colliezi*, side views, × 100**
6 ***Saracenaria sublaevis sublaevis*, oblique side view, × 100**
7 ***Dentalina matutina*, side view, × 45**

(continued overleaf)

Plate 11 *(continued)*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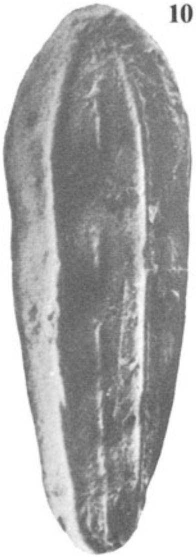
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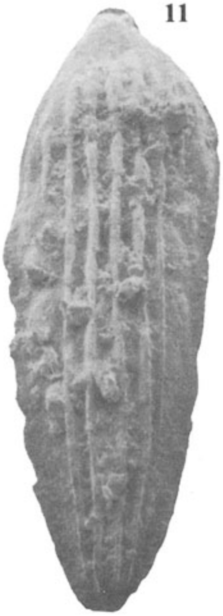
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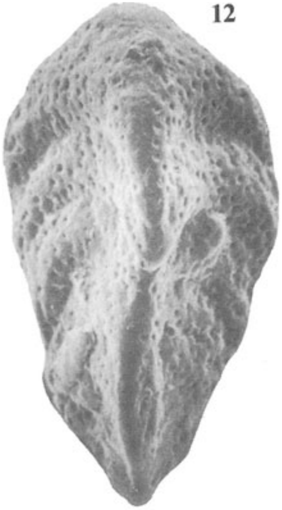
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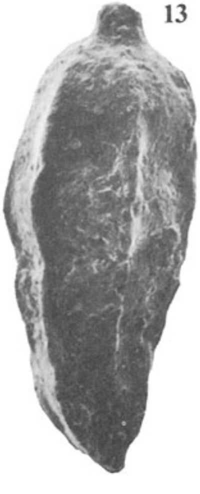
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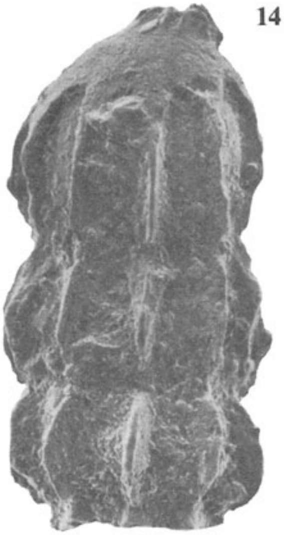
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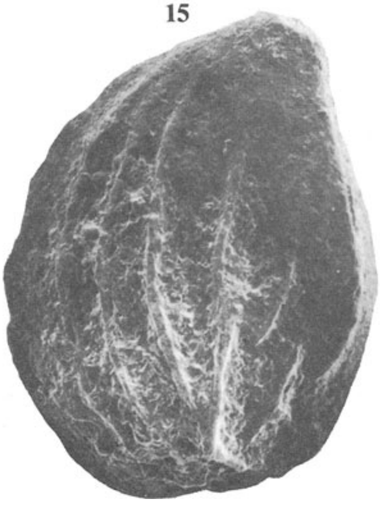
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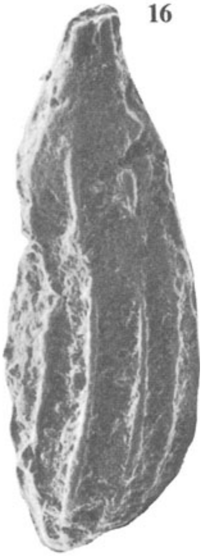
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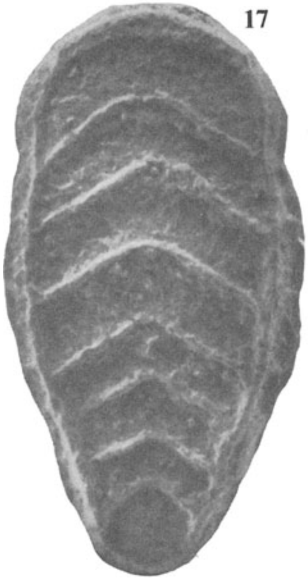
9 *Frondicularia terquemi muelensis,* **side view showing fine, dense ribbing, × 152**
10 *Lingulina tenera tenera,* **side view showing central ribs and sulcus, × 100**
11 *Frondicularia terquemi mediumcostata,* **side view showing central ribbing, × 76**
12 *Tristix liasina,* **side view, showing coarse perforation, × 200**
13 *Nodosaria issleri,* **side view, × 86**
14 *Marginula prima interrupta,* **side view showing interruption of the ribs over the sutures, × 156**
15 *Planularia inaequistriata,* **side view, × 136**
16 *Vaginulina curva,* **side view showing curved test intermediate with** *Astacolus,* **× 200**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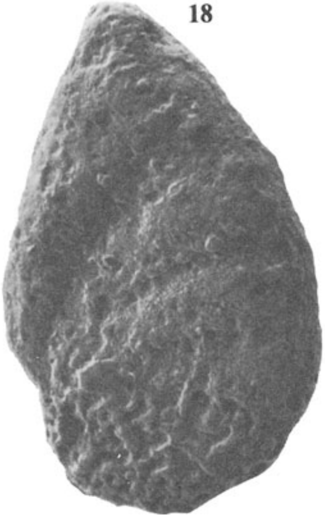
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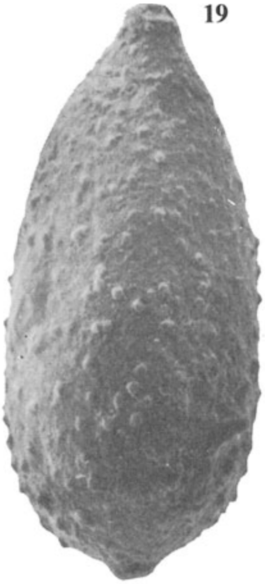
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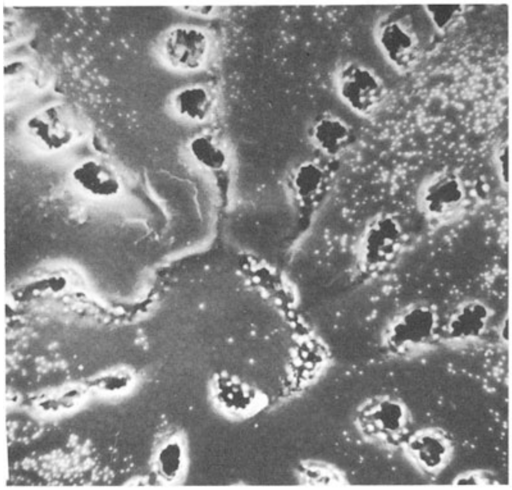
17 ***Lingulina tenera occidentalis,*** **side view showing raised sutures, × 200**
18 ***Astacolus (Planularia), semireticulata,*** **side view showing ornament, × 200**
19 ***Lagena liasica,*** **side view showing hispid texture and basal spine, × 200**

PLATE 12 *Internal structures of some rotaliids*

1



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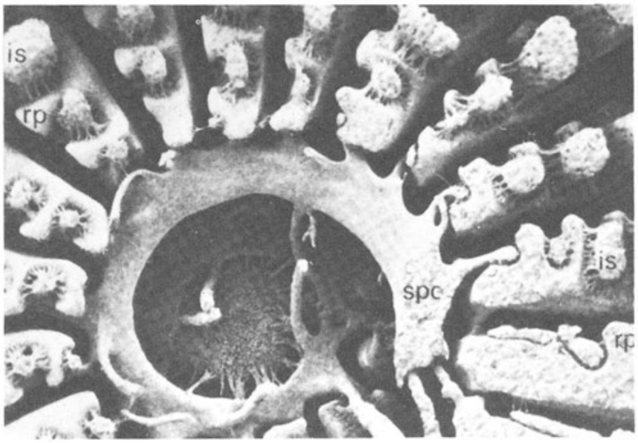

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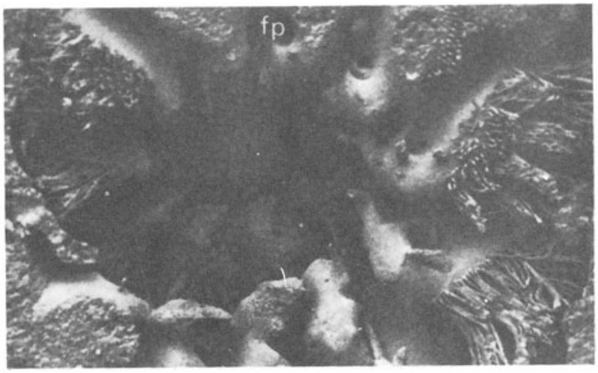

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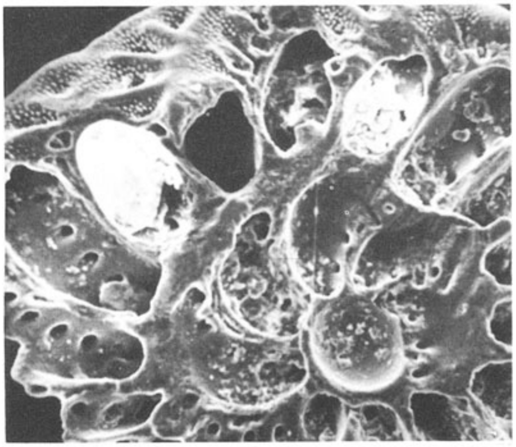

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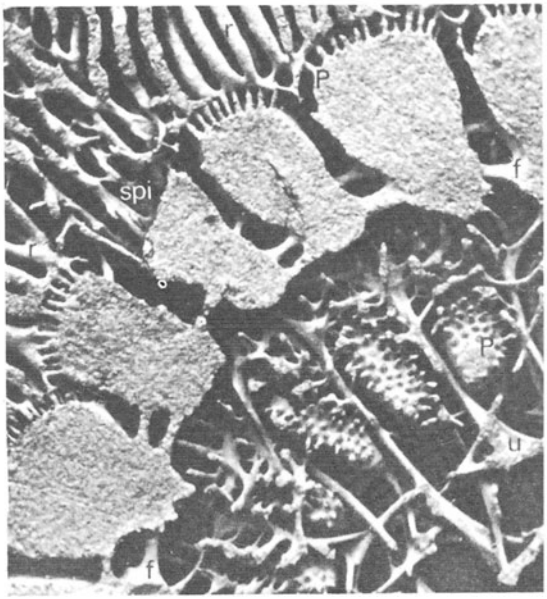

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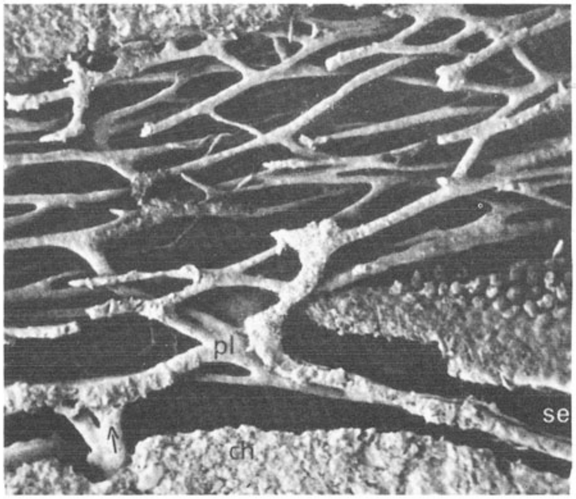


(all photography by SEM)

1 **Umbilical area of *Elphidium exoticum;* exterior view, showing septal bars (some with proximal openings) and septal pits leading to the 'interlocular spaces', × 392**

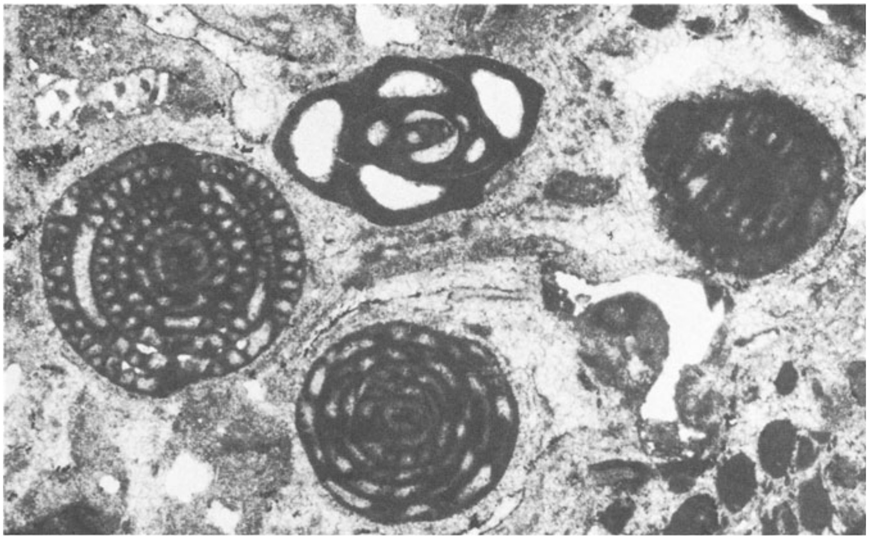
2 **Umbilical area of *Elphidium* sp.; cast of cavities, showing interlocular spaces (is), retral processes (rp) and spiral umbilical canal (spc). Note also the vertical umbilical canals and intraseptal canals, × 216. From Hottinger (1978)**

3 **Umbilical area of *Ammonia beccarii;* cast of cavities, showing presence of foraminal plate (fp) and absence of spiral umbilical canal, × 216. From Hottinger (1978)**

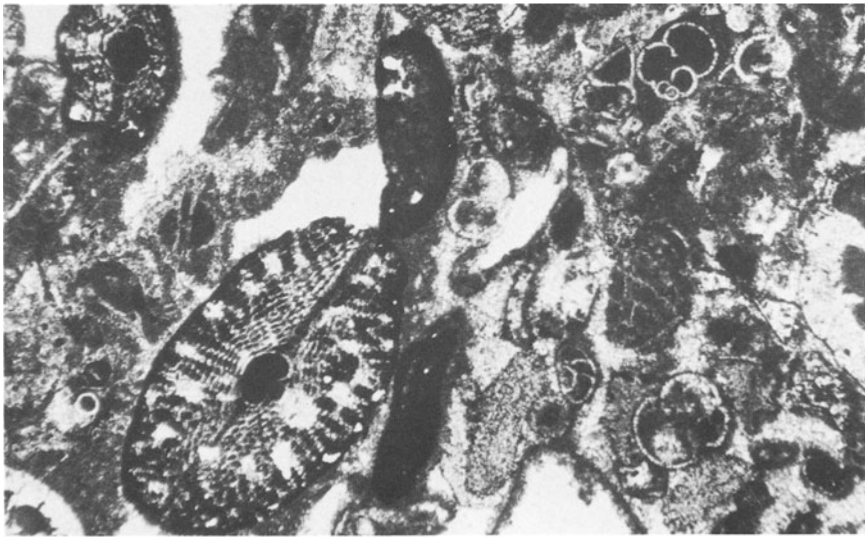
4 **Breached specimen of *Elphidium macellum,* showing septal pits and bars on upper surface with interlocular space formed by 'double septum' and entrances to the retral processes on internal surface, × 252**

5 **Cast of internal cavities in *Calcarina* sp., showing multiple intercameral foramina (f) and dorsal insertion of spine canals (spi), pores (P), radial canals (r) and umbilical canals (u), × 108. Vertical section from Hottinger (1978)**

6 **Cast of marginal canal system in *Operculina cummingii,* showing chamber cavity (ch), plexus (pl) connecting interseptal canal system, septum (se), with the marginal canal system. Arrow marks passage between chamber lumen and the canal system, × 540. From Hottinger (1978)**

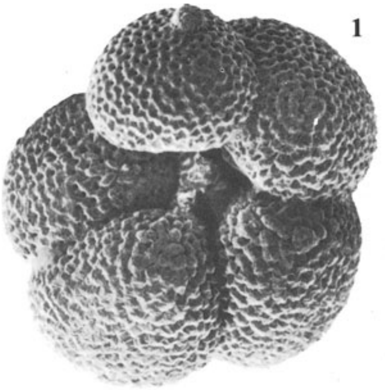


Limestone with *Borelis* sp. and associated miliolids and encrusting algae in a clear calcite matrix. Axial section of *Borelis,* showing 'Y-shaped' septa left, median section lower centre, section of *Quinqueloculina* centre top, fruiting body of dasycladacean alga lower right corner. From M. Miocene, Sirtica, Libya. Photomicrograph by ordinary light, × 29



Shelly foraminiferal/bryozoan limestone with *Asterocyclina* sp. cf. *A. soldadensis.* Axial section lower left, showing bilocular embryon and planktonic forams including *Globigerinatheka index,* lower right. Note that specimens have been transported and coated as well as impregnated with iron compounds (showing black). Although the limestone is of probable Oligocene age the contained (derived) species are of Upper Eocene age. From Porcupine Bank, N.E. Atlantic. Photomicrograph by ordinary light, × 20

Characteristic globigerinids: Globigerinacea, Hantkeninacea, Hedbergellacea **PLATE 14**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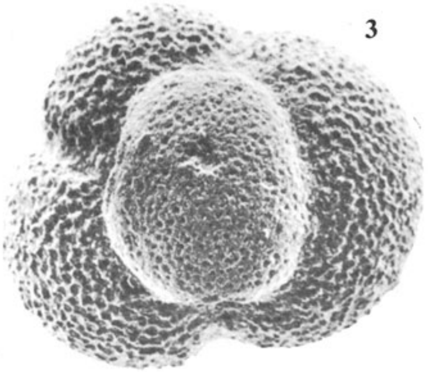
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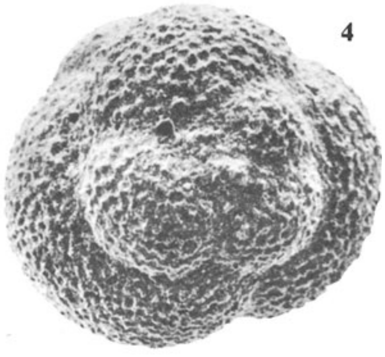
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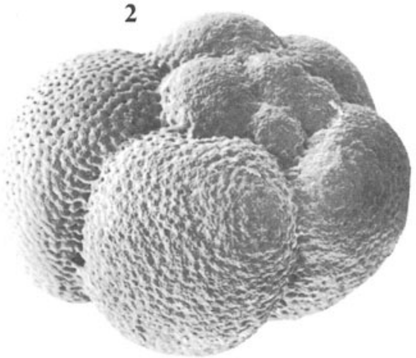
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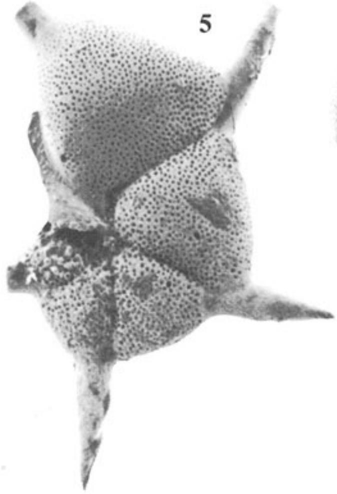
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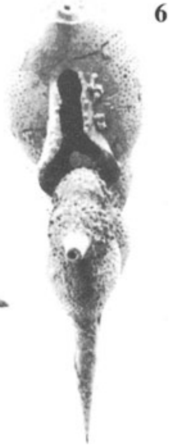
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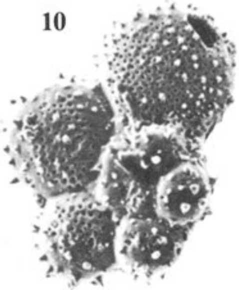
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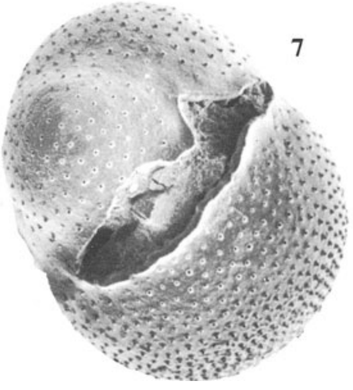
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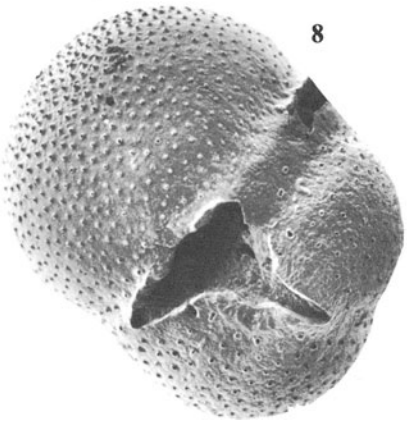
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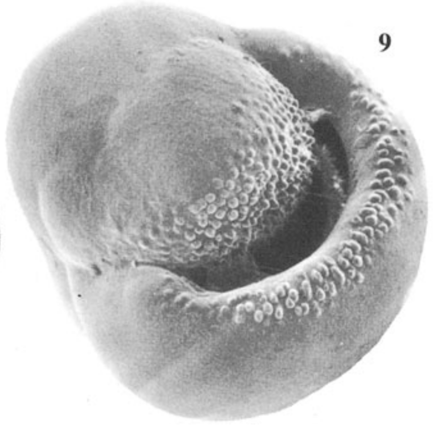
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(all photography by SEM)

1/2 *Neogloboquadrina dutertrei*, **ventral view, showing umbilical area and oblique dorsal view, × 100. Note growth of calcite rhombs which tend to mask original cancellate texture**

3/4 *Globigerinatheka index*, **ventral view, showing bulla and dorsal view, × 100**

5/6 *Hantkenina alabamensis*, **side and peripheral views, showing the aperture, × 100**

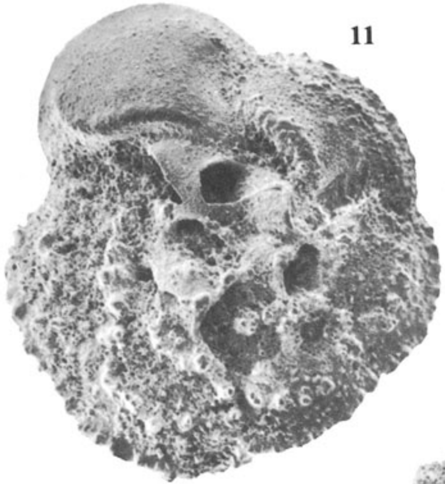
7/8 *Sphaeroidinella dehiscens*, **oblique and ventral views, × 75**

9 *Pulleniatina obliquiloculata*, **oblique apertural view, × 75**

10 *Hedbergella amabilis*, **dorsal view, showing short spines giving rugose texture and tendency to development of a poreless peripheral band, × 100**

(continued overleaf)

Plate 14 ***(continued)***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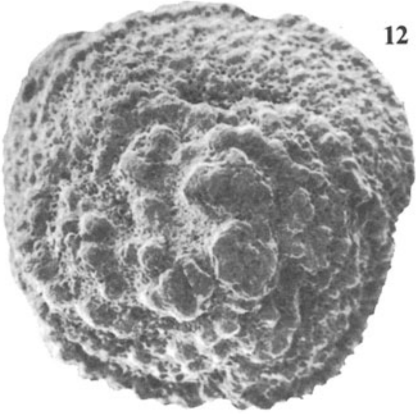
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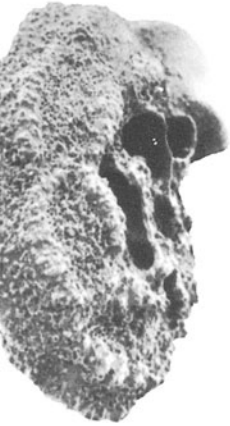
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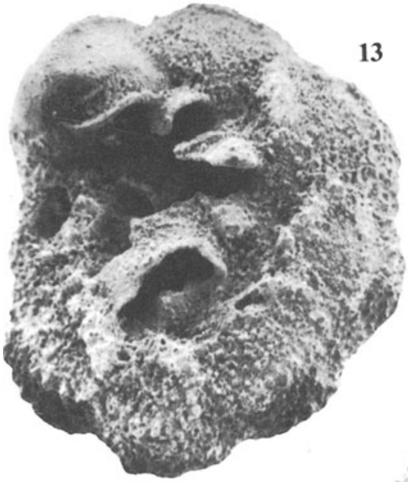
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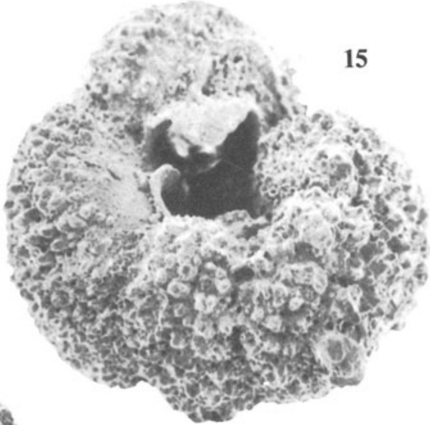
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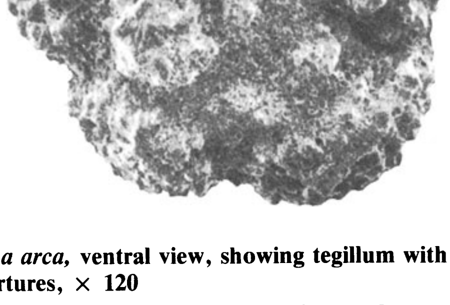
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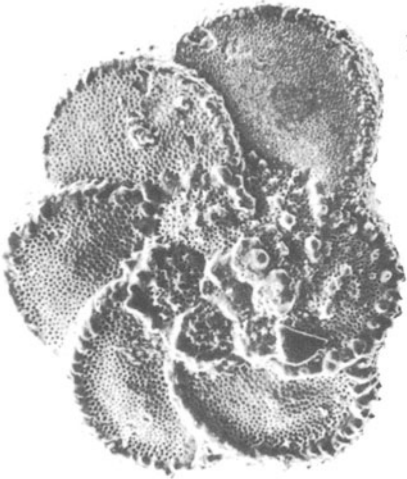
11 *Globotruncana arca,* ventral view, showing tegillum with areal and marginal accessory apertures, × 120

12 *Globotruncana contusa,* dorsal view, showing moderate spire and rugose ornament, × 120

13/14 *Globotruncana* sp., ventral and oblique peripheral views, showing broken tegillum and truncate periphery, × 100

15/16 *Rugoglobigerina pennyi,* ventral and dorsal views, showing rounded periphery and rugose ornament, tegillum broken, × 120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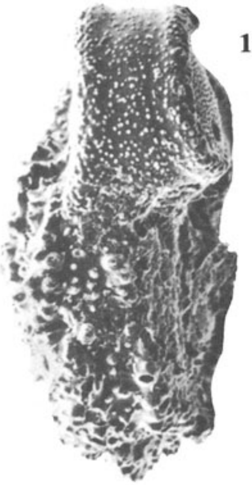
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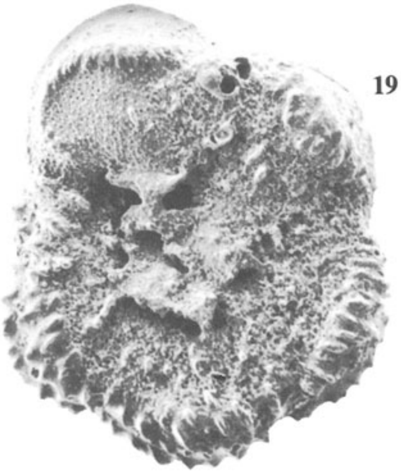
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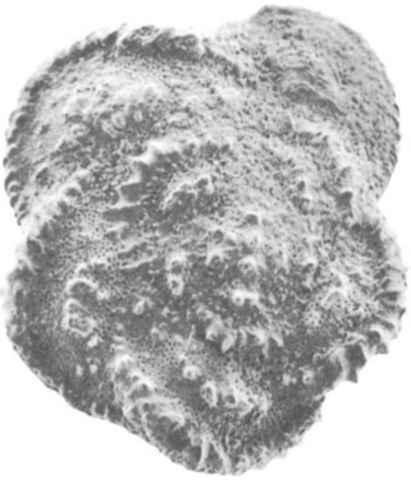
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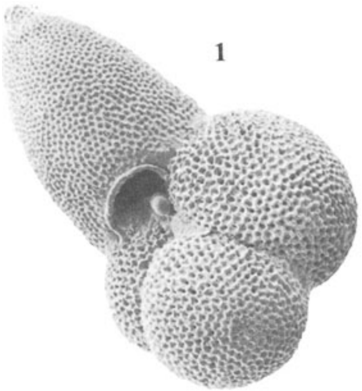
17/18 ***Globotruncana linneana,*** **dorsal and peripheral views, showing flattened, tabular form and wide poreless peripheral band, × 100**

19/20 ***Abathomphalus mayaroensis,*** **ventral and dorsal views, showing tabular form, techo with areal and marginal accessory apertures and short marginal costae (costellae), × 120**

PLATE 15 *Quaternary planktonic Foraminifera, tropical province*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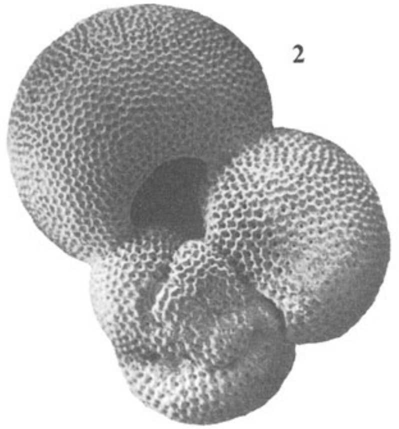
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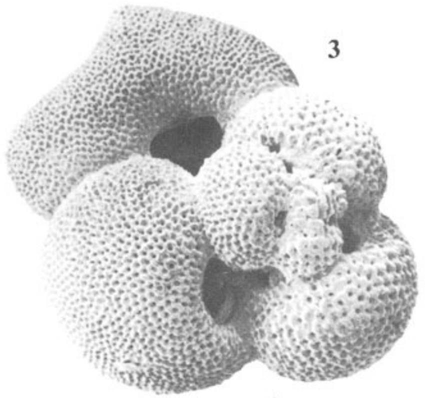
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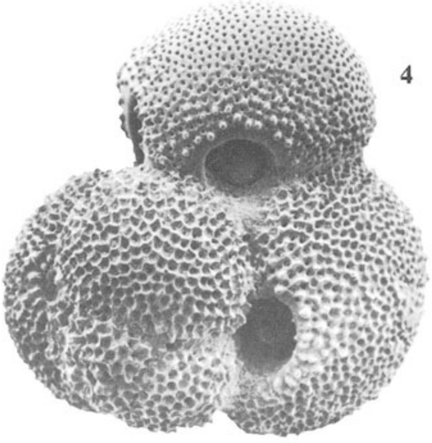
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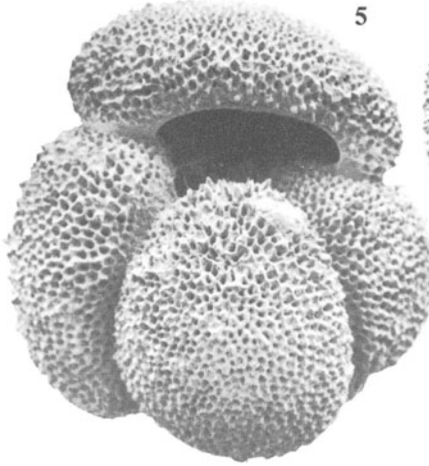
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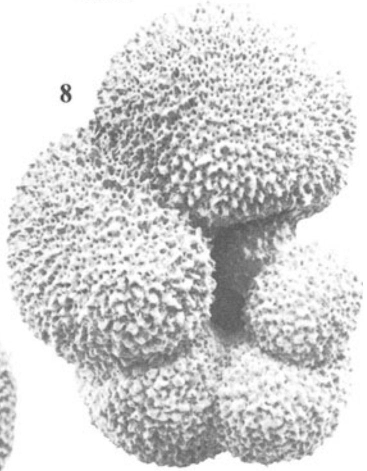
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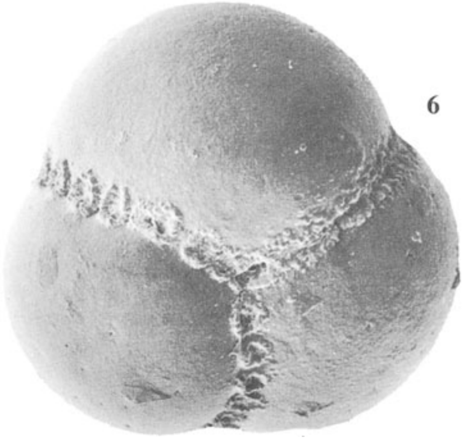
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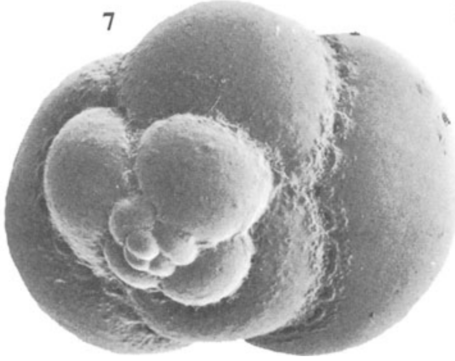
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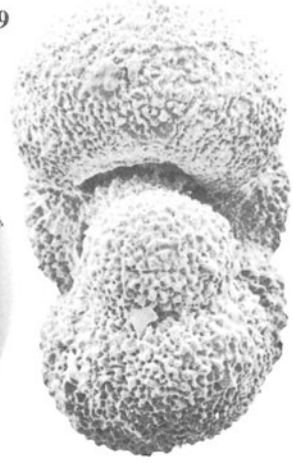
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(all photography by SEM)

1–3 *Globigerinoides sacculifer,* ventral view showing apertural lip and dorsal views showing supplementary apertures—one per chamber, × 50

4 *Globigerinoides ruber,* dorsal view, showing supplementary apertures—two per chamber, × 100

5 *Globigerinoides conglobatus,* ventral view, showing depressed, bun-shaped adult chambers, × 75

6/7 *Candeina nitida,* ventral and dorsal views, × 75

8/9 *Globigerinella aequilateralis,* side and peripheral views, × 100

Plate 15 ***(continued)***

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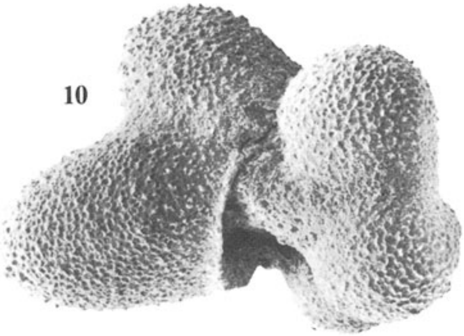

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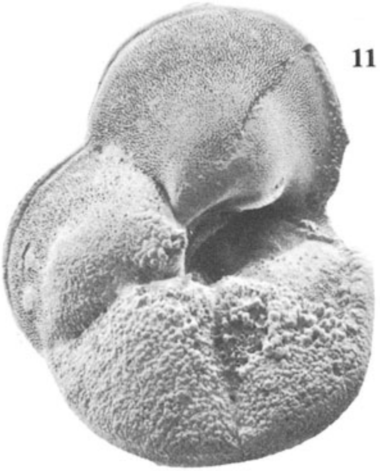

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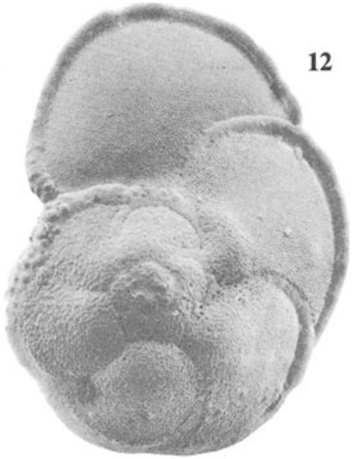

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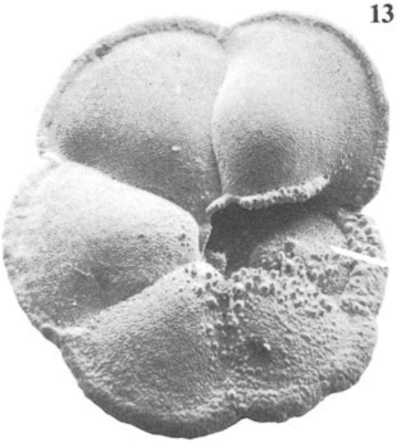

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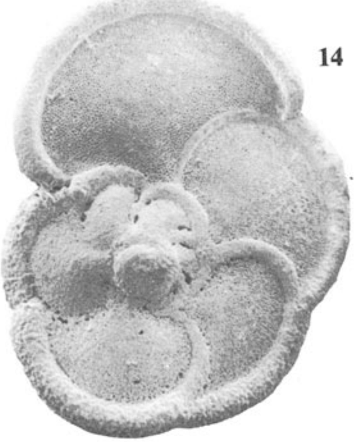

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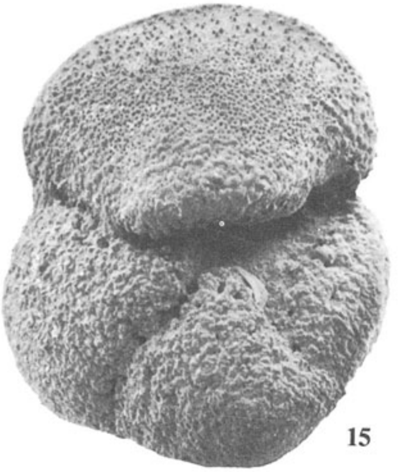

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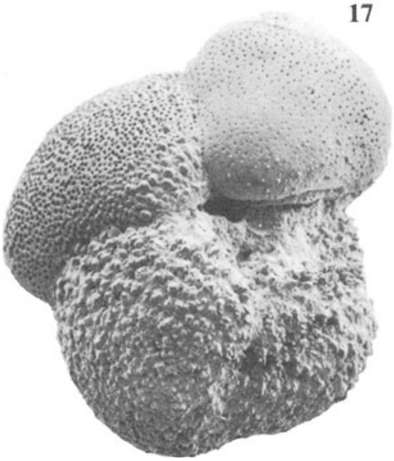

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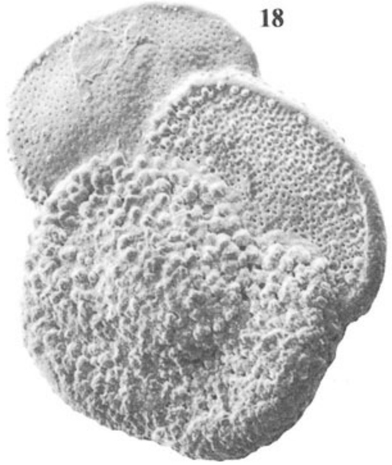

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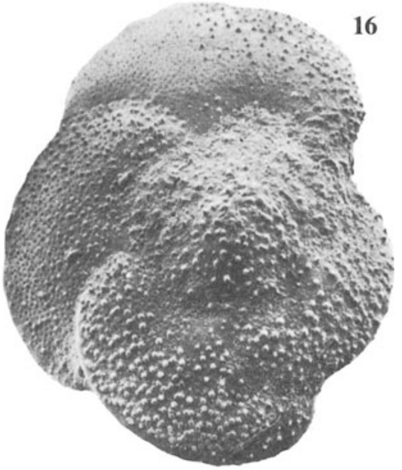

10 *Beella digitata*, oblique view, × 100
11/12 *Globorotalia tumida*, ventral and dorsal views, × 50
13/14 *Globorotalia cultrata* (= *menardii* of authors), ventral and dorsal views, × 50
15/16 *Globorotalia hirsuta* ventral and dorsal views, × 75
17/18 *Globorotalia crassaformis*, ventral and dorsal views, × 75

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SUMMARY CLASSIFICATION

MAIN FAMILIES AND IMPORTANT GENERA OF ROBERTINIDA

ROBERTINIDA n. order	wall aragonitic, radial; Trias. – Rec. Key figure 11.3.
DUOSTOMINACEA Brotzen 1963	planispiral or low to high trochospiral; aperture ventral umbilical or extra-umbilical to median, double or with distal arch and proximal fold or notch on either side of a lobe, may be a simple arch; M. Trias. – U. Jur.
DUOSTOMINIDAE	low trochospiral with numerous chambers in each whorl, dorsal side evolute, ventral side involute, aperture double with lobe and proximal and distal openings, crenulate; M. Trias.
Diplotremina (nos. 1/2)	open umbilicus and rounded periphery; apertures umbilical and extra-umbilical; M. Trias.
Duostomina (nos. 3 – 5)	closed umbilicus and angular periphery; apertures extra-umbilical; horizontal, arched partitions cut off access to foramina except at periphery and divide chamber; M. Trias.
ASYMMETRINIDAE	low trochospiral to planispiral, involute; aperture basal, a ventro-peripheral to median arch, crenulate; U. Trias.
Asymmetrina (nos. 7/8)	asymmetric planispiral, periphery angular; aperture median, irregular; U. Trias (Rhaet.).
Plagiostomella (no. 6)	low trochospiral to planispiral, rounded; sutures limbate; aperture a ventroperipheral arch; U. Trias (Rhaet.).
OBERHAUSERELLIDAE	low to high trochospiral with few chambers in each whorl, dorsal side evolute, ventral side involute; aperture umbilical or umbilical to extra-umbilical, with lip or with lobe and re-entrants; M. Trias. – U. Jur.
Oberhauserella Fuchs 1967 (nos. 9 – 11)	low trochoid with open umbilicus; aperture umbilical, beneath lobe, with distal arch and proximal fold; M. Trias. – U. Jur. (test moderately high, aperture with proximal notch only = *Praegubkinella* Fuchs 1969, Trias.).
Globuligerina Bignot and Guyader 1971 (no. 14)	low trochoid with closed umbilicus; aperture umbilical beneath lobe with distal arch and proximal notch; U. Jur. (periphery angular and aperture extra-umbilical = *Jurassorotalia* Fuchs 1973).
Conoglobigerina (nos. 12/13)	high trochoid; aperture umbilical, high arch with lip; M. – U. Jur. (large, open umbilical area, *Polskanella* (nos. 15/16) Fuchs, 1973). N.B. Affinity of these genera with other oberhauserellids is doubtful.*
CERATOBULIMINACEA	low trochospiral; narrow toothplate or partition partially blocking communication between the aperture and the secondary foramen; Jur. – Rec.
CONORBOIDIDAE	slightly umbilicate to umbilicus closed; aperture umbilical to extra-umbilical with lobe, distal arch and proximal fold or notch; pillar-like toothplate; L. Jur. – L. Cret.

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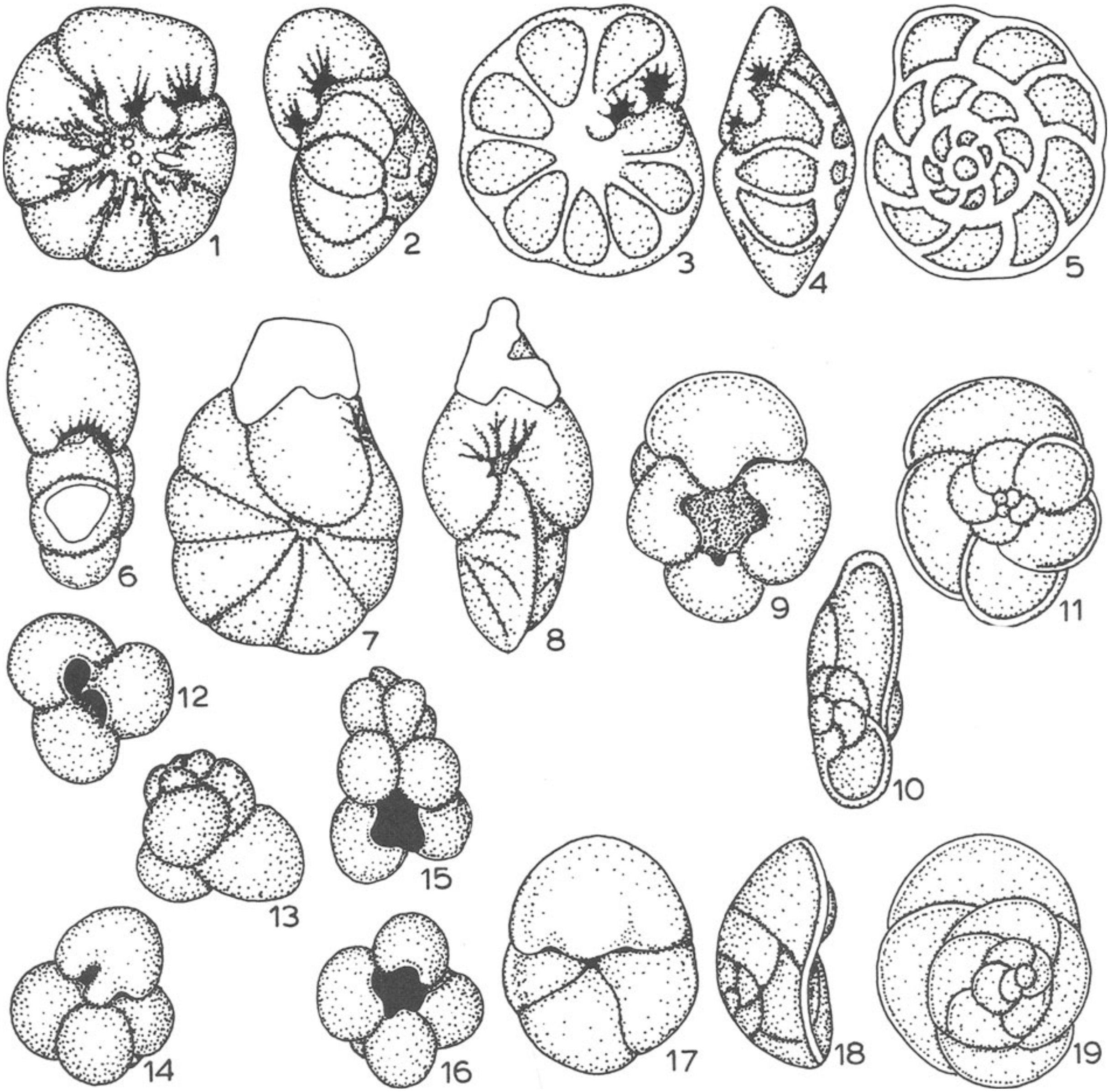
*See Grigelis and Gorbatchik (1980). *J. Foramin. Res.*, **10**(3):180 – 190.

Conorboides (nos. 17 – 19)	slightly umbilicate, aperture with low distal arch, short broad lobe and only slight proximal fold; L. Jur. – L. Cret.
Reinholdella (nos. 20 and 24)	umbilicus closed, aperture with low arch, narrow lobe and marked proximal notch which is closed with glassy plate in earlier chambers; L. – M. Jur.
EPISTOMINIDAE	umbilicus closed; aperture a peripheral or ventral, marginal slit; broad toothplate attached to ventral side of chamber, may join as partition, in plane of coiling or oblique; coiling mostly sinistral; Jur. – Rec.
Epistomina (nos. 21 – 23)	aperture marginal, closed in earlier chambers by secondary calcite; toothplate broad and curved, not reaching ventral wall, present throughout test; secondary foramen areal; Jur. – Cret. (toothplate in last chamber only, foramen basal = *Hoeglundina,* Cret. – Rec.; aperture peripheral = *Mironovella* Dain 1970, U. Jur. – L. Cret.; partition to ventral wall = *Epistominita,* U. Jur. – L. Cret.; aperture peripheral also = *Epistominoides* (nos. 25/26), Jur. – Eoc.).
CERATOBULIMINIDAE	deeply umbilicate, chambers increasing rapidly in height or length as added, mainly dextral; aperture umbilical to extra-umbilical; partition below central areal foramen, largely closing off apertural area; L. Cret. – Rec.
Ceratolamarckina (nos. 30 – 32)	aperture umbilical, wide with notched flap; partition flat with curved edge, attached below areal foramen and partly to ventral wall leaving crescentic, dorsal opening; L. Cret. – Palaeocene (angular periphery and flat ventral side = *Lamarckina,* U. Cret. – Rec.; partition marked on exterior by sutures = *Ceratocancris* (no. 29), Mio.).
Ceratobulimina (nos. 27/28)	aperture umbilical with deep central slit; partition marginally serrate, joined to ventral wall near apertural slit and bending round it to join dorsal wall, leaving small, crescentic, ventroperipheral passage only; U. Cret. – Rec.
ROBERTINACEA	high to low trochospiral, planispiral or asymmetrically uncoiled; partition formed by infolding of wall to give a supplementary chamberlet; foramen primary; Eoc. – Rec.
ROBERTINIDAE	high to low trochospiral asymmetrically uncoiled; aperture umbilical; Eoc. – Rec.
Robertina (nos. 33/34)	drawn-out trochospire of globular chambers; aperture a deep slit extending into the apertural face from the umbilicus, supplementary aperture at junction of secondary suture and basal suture on opposite side; Eoc. – Rec. (aperture opening beneath lobe with proximal extension into apertural face and distal extension along secondary suture = *Robertinoides* (no. 35), Rec.; low trochoid with rapidly enlarging chambers also = *Pseudobulimina,* Eoc. – Rec.).
Geminospira (no. 36)	trochospiral to uncoiled asymmetric; secondary chamberlets visible from both sides; aperture opening beneath lobe with distal extension along

	secondary suture and narrow, proximal extension into apertural face, broadening into ovate opening; Plio. – Pleist. (secondary chamberlets visible only on ventral side and aperture with short, proximal notch passing into groove = *Cerobertina,* M. Eoc. – Rec.).
ALLIATINIDAE *nom. transl.* McGowran 1966	low trochospiral to planispiral; aperture ventral basal to median with additional areal opening; Neo.
Alliatinella (no. 39)	low trochoid, later chambers high; supplementary chamberlets visible on ventral side only; partition chevron-shaped; ventral areal aperture connected by suture to base (may be closed with glassy plate); Plio.
Alliatina (nos. 37/38)	planispiral; supplementary chamberlets visible on both sides; partition a narrow, inverted-V; areal and basal apertures in median line (peripheral); Plio. – Pleist. (glassy, poreless zone above areal aperture and partition reduced to inverted split-tube with branches to supplementary apertures = *Cushmanella,* Rec.).



Key figure 11.3 Robertinida

1/2 *Diplotremina astrofimbriata* **Kristan-Tollmann, ventral and peripheral views, × 125**

3 – 5 *Duostomina biconvexa* **Kristan-Tollmann, ventral, peripheral and dorsal views (in clarifier), × 125**

6 *Plagiostomella inflata* **Kristan-Tollmann, apertural view, × 125**

7/8 *Asymmetrina biomphalica* **Kristan-Tollmann, side and apertural views, × 80**

9 – 11 *Oberhauserella quadrilobata* **Fuchs, ventral, peripheral and dorsal views, × 150**

12/13 *Conoglobigerina dagestanica* **(Morozova), ventral and peripheral views, after Fuchs, × 100**

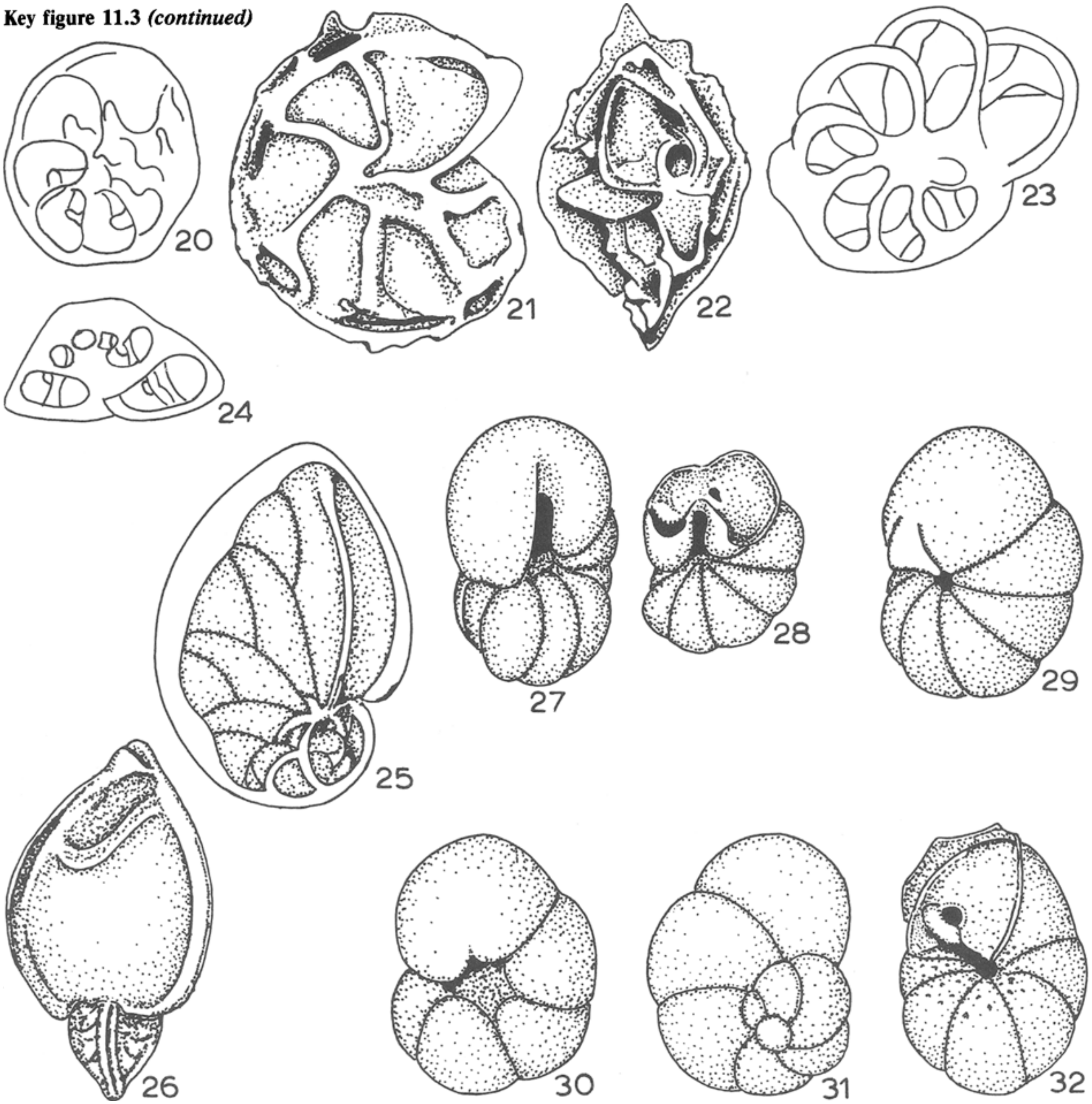
14 *Globuligerina frequens* **Fuchs, ventral view, × 100**

15/16 *Polskanella altispira* **Fuchs, peripheral and ventral views, × 100**

17 – 19 *Conorboides mitra* **(Hofker), ventral, side and dorsal views, after L. & T., × 87**

(continued overleaf)

Key figure 11.3 *(continued)*



20 *Reinholdella dreheri* (Bartenstein), ventral side, after Hofker, × 70

21 – 23 *Epistomina spinulifera* (Reuss), ventral and peripheral views, after Dam, × 50; 23 ventral view in clarifier to show toothplates, after Hofker, × 36

24 *Reinholdella dreheri* (Bartenstein), ventral view in clarifier to show toothplates, after Hofker, × 7

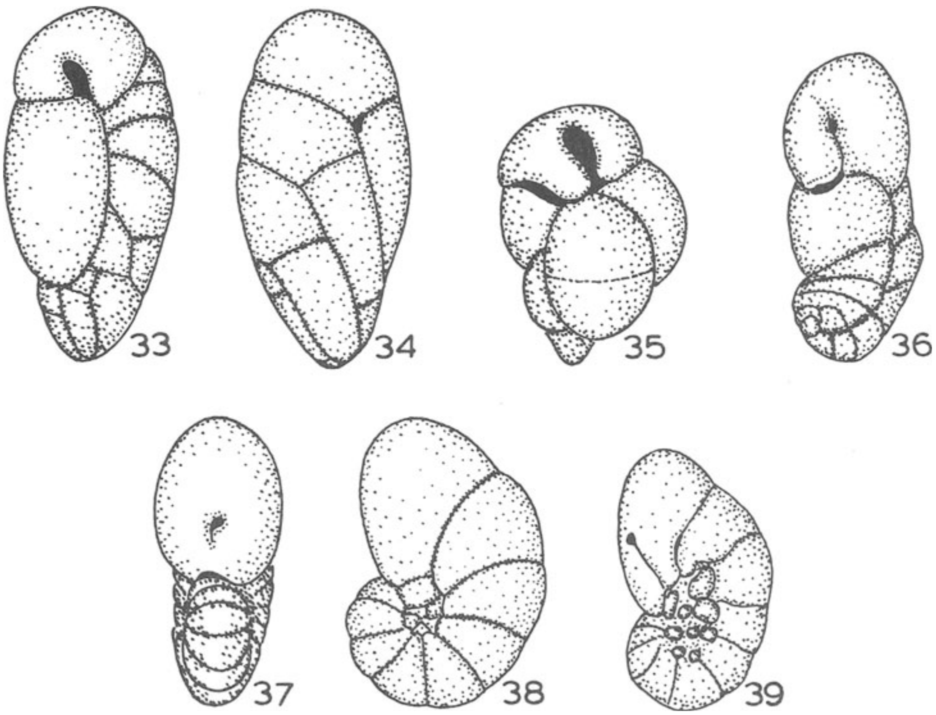
25/26 *Epistominoides wilcoxensis* (Cushman & Ponton), side and apertural views, after L. & T., × 93

27/28 *Ceratobulimina contraria* (Reuss), ventral views, after L. & T.; 28 dissected to show partition, × 90

29 *Ceratocancris clifdenensis* (Finlay), ventral view, after L. & T., × 70

30 – 32 *Ceratolamarkina tuberculata* (Brotzen), ventral and dorsal views, after L. & T., × 115; broken specimen showing areal foramen, after Haynes, × 100

Key figure 11.3 ***(continued)***



33/34 ***Robertina arctica*** **d'Orbigny, front and rear views, after L. & T., × 75**
35 ***Robertinoides normani*** **(Göes), front view, after Höglund, × 50**
36 ***Geminospira simaensis*** **Makiyama & Nakagawa, side view, after L. & T., × 105**
37/38 ***Alliatina excentrica*** **(Napoli Alliata) after L. & T., apertural and side views, × 119**
39 ***Alliatinella gedgravensis*** **Carter, ventral view, × 92**

Chapter 12

The Rotaliida (Smaller)

> The (rotaliids) are found in all of the known marine habitats where Foraminifera occur, warm, cold, shallow or deep water and pelagic.
>
> (Galloway, 1933)

The Rotaliida are the most abundant order in numbers of genera, penetrating most marine environments but especially characteristic of shelf seas. Although mainly trochoid they show the greatest range of coiling modes with many specially adapted for a fixed life on hard, current-swept substrates, including the assumption of arborescent growth resembling that of bryozoans together with bright colours. Exploitation of lamellar bonding is carried furthest in the group also with the development of a canaliculate, annular complex test along a number of different lines. Wall structure is hyaline calcareous and includes radial and oblique arrangement, or is compound. The test may also consist of a single crystal. The shallow water genera are commonly symbiotic with algae and some are known to subsist entirely by this means (see chapter 3).

As in the case of the Miliolida the ecological relationships of the rotaliids in the present oceans have received much attention. As they also show marked evolutionary trends, particularly through the Cenozoic, they are a prime tool in biostratigraphical analysis of the younger rocks.

As the order is very large it is convenient to discuss the families which are composed mainly of small genera in a separate chapter from the larger rotaliids. This is illogical to the extent that families of larger forms include small ancestral forms, such as *Rotalia* in the Rotalidae. It also leads to artificial groupings where the ancestors of certain large genera are unknown. However, it reflects the fact that the larger rotaliids are generally separately treated in the literature, often by specialists who have devoted their entire working lives to the study of certain families or even only one.

As might be expected, the study of small rotaliids goes back to the time of the earliest investigations of Tertiary Foraminifera in Europe, and a considerable number of genera were illustrated by models to accompany d'Orbigny's 'Tableau méthodique' (1826). Classic studies were also made by Roemer (1838), Bornemann (1855) and Reuss (1856 – 70) in Germany and Belgium, especially on the famous Oligocene 'Septarian Clays', by d'Orbigny (1846) on the Miocene of the Vienna Basin, by Jones, Parker and Brady (1866) on the Plio-Pleistocene 'Crags' of Britain, and by Terquem (1882) on the Eocene of the Paris Basin.

CHAMBER FORM AND COILING MODES

Besides being the most diverse and abundant order (some 256 genera), the Rotaliida also show the greatest range of coiling modes (figure 4.3). However, low trochospiral chamber arrangement is clearly dominant (40 per cent with an additional 5 per cent conical) followed by planispiral arrangement (18 per cent). Annular complex arrangement reaches 14 per cent and annular discoid arrangement 8 per cent. Other modes occur at less than 5 per cent. This makes a striking contrast with the Lituolida and Buliminida.

If the families of small rotaliids are taken on their own (70 per cent of the order), low trochospiral arrangement reaches 51 per cent while planispiral arrangement is only slightly reduced to 17 per cent. Annular discoid arrangement is also almost as common (7 per cent) but annular complex arrangement is reduced to 1 per cent, showing how this type is closely related to size. A relatively high proportion are apparently permanently attached forms, including the arborescent genera and a number of trochoid and annular discoid forms, many becoming irregular.

The superfamilies and families are recognised on the basis of chamber arrangement and apertural and umbilical characters. Some families also show stability of wall structure. See the Summary Classification at the end of the chapter.

Spirillinacea

This superfamily includes planispiral to conical, unilocular to biserial genera. The unilocular genera are included in the Spirillinidae. Here the aperture is formed by the open end of the tube. The biserial genera are included in the Patellinidae and in this case the aperture is ventral basal and opens beneath an umbilical lobe. Incipient chamberlets occur in *Patellina.* As discussed in chapter 4, both *Spirillina* and *Patellina* have tests composed of a single crystal of calcite. For this reason, apparently hyaline oblique, unilocular genera such as *Involutina* and *Trocholina* were placed in a separate family, Involutinidae, in the 'Treatise'. These genera are homeomorphs of *Spirillina* and *Turrispirillina* but differ in possessing umbilical fillings. According to Hohenegger and Piller (1975, 1977) these genera are aragonitic so should be included in the Robertinida as here understood.

Discorbacea

Trochoid genera with three or more chambers in each whorl and umbilical to extra-umbilical aperture on the ventral side are included in this superfamily. Four main families can be recognised. In the Discorbidae the aperture opens beneath an umbilical extension of the last chamber (lobe or tenon) with a distal arch and a proximal notch. The ventral side is generally flattened or concave, often with the umbilicus secondarily closed by a boss, irregular secondary calcite, or by fusion of the successive umbilical lobes. In the Cancrisidae the test is biconvex with raised ventral side and the umbilicus is wholly covered by a lobe extending from the last chamber or by the successive umbilical flaps of the chambers in the last whorl. In contrast, the aperture is a simple, umbilical opening in the Bagginidae. A more complicated structure is developed in the Cymbaloporidae in which the adult is conical with multiple, ventral apertures—possessing annular rings of alternating chamberlets or annular chambers with partitions, as in *Fabiania,* which achieves 'large foraminifer' size.

The wall varies at the generic (and possibly specific) level in the Discorbidae and Cancrisidae, whereas the Bagginidae and Cymbaloporidae appear to be hyaline radial.

Asterigerinacea

In this superfamily the umbilicus is closed and the aperture is ventral and basal or areal (Eponididae), with extensions or folds in the apertural face (Alabaminidae) or marginal to siphonate (Siphoninidae). The Asterigerinidae have supplementary chamberlets produced by development of a toothplate in the ventral, umbilical area and the aperture is a simple, ventral basal arch.

The position of the Alabaminidae is problematical but they are included here for the time being (but *Gyroidina* is transferred to the Cancrisidae because of apertural differences).

Amphistegina was placed close to *Asterigerina* by Cushman (1948) and Glaessner (1945, see reprint 1963a; 1963b), but these genera were separated in the 'Treatise'. Detailed work by SEM (Hansen and Reiss, 1972b) has shown that these genera have 'an essentially identical test construction and wall structure'.

Most genera in this superfamily are trochoid and biconvex but planispiral arrangement occurs in the Asterigerinidae and uncoiling in the adult stage occurs in both the Siphoninidae and the Eponididae. Both hyaline radial and hyaline oblique wall structure occurs in the Alabaminidae and Siphoninidae, but the Asterigerinidae and Eponididae are apparently radial.

Orbitoidacea

Most genera in this superfamily are permanently attached and there is a marked change in habit compared with the other superfamilies of small rotaliids in that the flat surface of attachment is formed by the evolute, 'dorsal' side of the spire. In sympathy with this change the aperture extends over the periphery and typically extends along the spiral suture on this side.

The Anomalinidae includes low trochospiral to almost planispiral genera (Anomalininae) and planoconvex to irregularly uncoiled and annular genera (Cibicidinae). The attempt was made in the 'Treatise' to separate these groups at the family level on the basis of wall structure, but this has foundered because variation occurs at both the generic and specific level with all the types found in the superfamily, hyaline radial, oblique, intermediate and compound. Genera with ventral apertures or ventral to peripheral apertures and open umbilicus, such as *Boldia, Gavelinella* and possibly *Discanomalina,* should be transferred to the Discorbacea.

Annular discoid architecture with rings of alternating chamberlets is exhibited by the Planorbulinidae, and the closely related Acervulinidae includes irregular and encrusting forms. Genera with irregularly trochoid to arborescent growth are included in the Homotrematidae.

Nonionacea

In this superfamily the chamber arrangement is trochospiral to involute planispiral with basal to median aperture. Most genera are planispiral and in advanced forms the aperture becomes multiple and areal.

Genera with closed umbilicus and trochospiral to involute planispiral coiling, with only a few chambers in each whorl, are included in the Chilostomellidae. In the Nonionidae, coiling is again trochospiral to planispiral but there are numerous chambers in each whorl and the umbilicus is open or secondarily closed with an extension lobe of the final chamber, by granules or by a single boss. In the Elphidiidae, the umbilicus is closed by fused umbilical flaps or is again granulate or embossed but in this case with intercommunicating umbilical cavities or fine vertical canals (canaliculate). The septal sutures are deeply fissured and in advanced forms become partially bridged by proximal extensions of the rear wall of subsequent chambers to form 'intercameral lacunae' or 'interlocular spaces'. Supplementary umbilical apertures open into these lacunae. In *Elphidium* and its allies, true septal bridges (externally marking internal development of retral processes) are developed, together with a partial septal flap. The lacunae now become septal canals connecting with a spiral canal around the umbilicus and communicating with the exterior via the umbilical canals and the septal pits along the sutures (plate 12).

These structural changes appear to have occurred in different stocks at different times. Also, although the structure of the wall appears to be consistently hyaline oblique in the Chilostomellidae and Nonionidae, both radial and oblique genera occur in the Elphidiidae. In some genera, such as *Haynesina* and *Elphidium,* variation occurs at the specific level (plate 7).

There has been almost continuous debate about the precise character and relative importance of these features since the pioneer work of Carpenter *et al.* (1862). Authors have made divisions on the basis of wall structure, aperture and internal features, including canals and retral processes, but have found them difficult to apply consistently at the generic level.

Cushman (1939), in his monograph on the Nonionidae, and Wade (1957) took a wide view of *Elphidium* but later workers took a more restricted view (Hofker, 1956; Ujiié, 1956; Voloshinova, 1958; Krashenninikov, 1960; Loeblich and Tappan, 1964), with recognition of a number of genera in the *Elphidium* group. More recently there has been a partial return to the wider viewpoint and Hansen and Anne-Lise Lykke-Anderson (1976) put *Cellanthus, Cribroelphidium* and *Cribrononion* in synonymy with *Elphidium* and also made *Florilus, Nonionellina* and *Protelphidium* synonymous with *Nonion.* On the other hand, Banner and Culver (1978) recognise *Florilus* and have redefined *Protelphidium* on the basis of umbilical characters which distinguish it from some other species of the *Nonion* group they now include in *Haynesina* (figure 12.1). Again, although Wade (1957) considered the lack of retral processes and the presence of a double (sometimes single) row of septal pits (outlets of diverging canals) insufficient grounds to separate *Elphidiella* from *Elphidium,* these genera were placed in separate families by Smout (1954). In this case, Hansen and Anne-Lise Lykke-Anderson (1976) consider that the 'connecting canals' to the septal pits cut the outer lamellae in *Elphidiella,* and therefore are fundamentally different from those in *Elphidium.*

More needs to be learned about the stratigraphical relationships of these genera before these problems can be resolved.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

There are two main theories concerning the origin of the Rotaliida. The older view is that the families of small rotalids descended from the Spirillinacea via the Discorbidae. Cushman (1948) considered that the Discorbidae sprang from *Patellina* whereas Glaessner (1945, see reprint 1963a), noting the abundance of *Spirillina* in the early Mesozoic and the late appearance and structural complexity of *Patellina,* favoured direct descent from a unilocular spirillinid and an ultimate origin in the Upper Palaeozoic unilocular forms — Archaediscina as here understood. The second, later suggestion, is that these families have descended from separate stocks of aragonitic Foraminifera. This radically different hypothesis was originally proposed by Hofker (1951, 1956). One

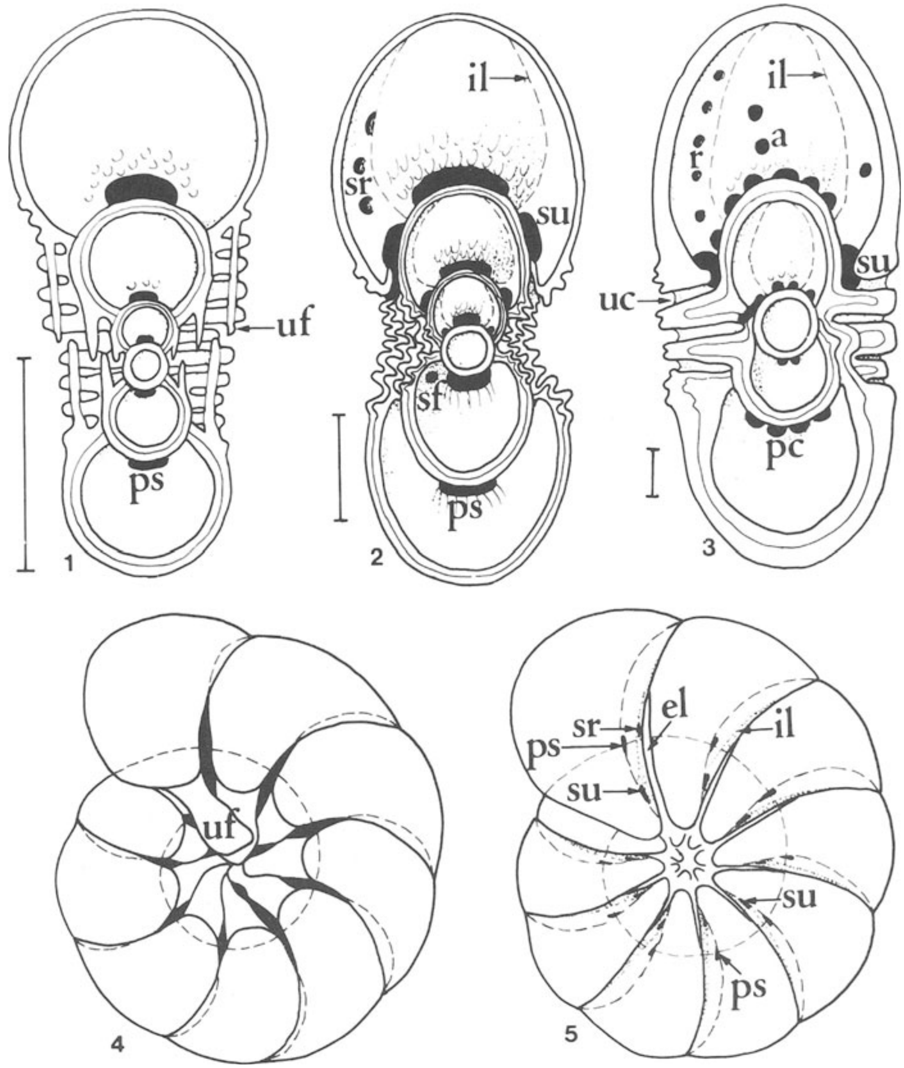


Figure 12.1 Diagrams to show the essential structural differences between *Protelphidium* Haynes (based on *P. hofkeri* Haynes), *Elphidium* de Montfort (based on *E. excavatum* (Terquem)), and *Haynesina* (based on *H. germanica* (Ehrenberg))

1 – 3 Idealised axial-sectional views:

1 *Protelphidium,* 2 *Haynesina,* 3 *Elphidium.* The upper half of each shows the anterior faces of septa, and the lower half shows posterior faces. The right-hand side of each diagram illustrates the essential characters of each genus; the left-hand side shows the maximum apertural and retral process-pit developments observed in the species used as models. In each case, the tubercular developments at the base of the septal aperture (on the anterior face) are omitted for clarity. The plurality of lamellae in the spiral wall is indicated but not accurately quantified. Relative magnifications are indicated by the scale bars, which represent the same length in each case (ca. 0.1 mm)

4 – 5 Idealised equatorial – lateral views of whole specimens:

4 *Protelphidium,* 5 *Haynesina.* All tubercules have been eliminated to clarify the umbilical differences. Sutures are delineated by continuous lines; anterior septal faces and the periphery of the penultimate whorl by discontinuous lines

Key: a areal septal aperture; el external opening of intercameral lacuna; il inner limit of intercameral lacuna (potential 'septal canal'); pc primary septal aperture (cribrate); ps primary septal aperture (single); r retral process pit; sf frontal supplementary aperture; sr retral supplementary aperture; su latero-umbilical supplementary aperture; uc umbilical channel (potential 'umbilical canal'); uf umbilical flap ('tenon'). From Banner and Culver (1978) group of rotalids, including the Discorbidae (Pulvinulinidae) and its offspring the Asterigerinidae and the Cymbaloporidae, is thought to be descended from *Conorboides* (suborder Deuteroforaminata, with reduced primary aperture). Another group is considered to have been derived from separate stocks within his suborder Biforaminata (with second aperture formed by a folded toothplate): the Alabaminidae, Eponididae and Cibicididae from the Ceratobuliminidae and the Nonionidae and Elphidiidae from the Robertinidae. A polyphyletic origin was therefore envisaged from different ancestors which have since been shown to be aragonitic—Robertinida as here understood.

In the 'Treatise', Loeblich and Tappan separated the Spirillinacea from the Discorbacea and in 1974 adopted the second viewpoint. The Discorbidae are considered to have sprung directly from the Oberhauserellidae and to have given rise to one line leading through the Eponididae to the Cibicididae, the Planorbulinidae, Cymbaloporidae and Acervulinidae, and another line leading to *Asterigerina* and *Amphistegina*. The Nonionacea, in which the Alabaminidae, Anomalinidae and Osangulariidae are included, are thought to have originated separately from the Asymmetrinidae. The Elphidiidae are removed to the Rotaliacea. A minor modification to this scheme was made by Helen Tappan (1976) in that the Cibicididae are considered to have arisen separately from early discorbids in the Jurassic.

Since the recognition of *Reinholdella* Brotzen (1948) and *Oberhauserella* Fuchs (1967), it has become clear that most, if not all, the references to *'Discorbis'* and *'Asterigerina'* in the Triassic and Jurassic in reality refer to members of the Duostominacea—see chapter 11. Further work is required but it seems likely that all the superfamilies of small rotaliids, apart from the Spirillinacea, arose in the Cretaceous. This removes the objection made by Glaessner on stratigraphical grounds to Cushman's suggestion that the Discorbidae arose from among the Patellinidae. The problem remaining here is the possibility of considerable genetic separation between genera in which the test is optically a single crystal and hyaline radial/oblique genera built of numerous rhomboid microcrystals. SEM work reveals that the apertures in the two families are much closer in form than originally thought by Loeblich and Tappan (Haynes *et al.*, 1973).

The main support for the derivation of the discorbids from *Oberhauserella*, apart from the circumstantial evidence provided by the replacement of the Duostominacea by the rotaliids in the late Mesozoic, is the close similarity in apertural form. In both cases the aperture opens beneath an umbilical flap with distal arch and proximal notch. However, the same apertural form is found in the agglutinated Trochamminidae. This prompted an earlier, alternative suggestion by Cushman (1948) that the rotaliids may have arisen from an agglutinated ancestor by this route. Likewise, Hofker sought for the ultimate origin of all the 'toothplate' Foraminifera in the Valvulinidae. The possibility must therefore be entertained that the Duostominacea and the Discorbacea could have arisen from the Ataxophragmiacea at different times.

There is no evidence from evolutionary studies to support one or other of the conflicting theories on the origin of the Rotaliida. The Spirillinacea are closer in wall structure to the Discorbacea than to any of the other groups regarded as ancestral, so it seems best on balance to take the conservative position. The Discorbacea are therefore considered to have arisen from among the Patellinidae with a possible ultimate origin in the Archaediscina.

A weakness in the idea that the Discorbidae are the rootstock from which the other families of the Discorbacea arose is the rarity of *Rosalina* and its allies in the Cretaceous and even in the Tertiary where small rotaliids as a whole are abundant. *Discorbis* s.s. is not known until the Eocene. However, work in Cardigan Bay (Dobson and Haynes, 1973) reveals that although members of the Discorbidae are abundant as epibionts, they are rare in death assemblages compared with the more robust rotaliids. This suggests that their apparent earlier rarity is caused by failure of the fossil record. All the other families appear in the Cretaceous but the Cymbaloporidae not until the Upper Cretaceous.

The main trends in the Spirillinacea are towards conical test shape and long, low chambers and even incipient chamberlets in the Patellinidae. In the Discorbacea the main trends are towards the development of various umbilical coverings on the excavated, open umbilical side—Discorbidae; biconvexity with the tendency for an extended lobe from the last chamber to become dominant as an umbilical cover and for the aperture to extend to the periphery—Cancrisidae; globularity with the development of surface ornament and especially radial striae around a simple, umbilical aperture—Bagginidae; annular conical arrangement with chamberlets and umbilical coverplates—Cymbaloporidae.

The Asterigerinacea apparently arose from the Discorbidae by closure of the umbilicus with migration of the aperture to an extra-umbilical position. This happened early in the Cretaceous as *Eponides* is present by the Albian. The main development of the Eponididae is, however, in the Tertiary with the appearance of cribrate apertures and one of the rare examples of uncoiled uniserial growth in the Rotaliida, in *Rectoeponides*. The Asterigerinidae appear to have sprung from the Eponididae in the late Cretaceous. Here again, the main development is in the Cenozoic with the appearance of *Asterigerina* s.s. and *Amphistegina* in the Eocene. The Eponididae may also have given rise to the Siphoninidae by migration of the aperture to a marginal position. *Pulsiphonina* gave rise to the siphonate *Siphonina* in the late Palaeocene and this family shows uncoiling trends in the Eocene. *Pulsiphonina* is hyaline oblique but the other genera are radial.

The Alabaminidae show a tendency towards extension of the aperture into the apertural face with resemblances to members of the Buliminida. The marginal fold in *Alabamina* could be taken to indicate the former presence of an aperture with toothplate, as in *Epistominella,* following the reasoning of Hofker. But the possibility also exists that this feature is not relict but has an adaptive function. In this case an origin within the Discorbacea is more probable.

The Orbitoidacea probably also arose from the *Eponides* group via *Heterolepa* in which the aperture becomes ventro-peripheral. The major trend is towards extension of the aperture along the spiral suture as a consequence of a switch in habit which brought the morphological, dorsal (upper) side into contact with the substrate.

There are two main Cretaceous developments in the Anomalinidae. One group, including *Anomalinoides,* remains biconvex, becoming almost planispiral (Anomalininae). This is presumably connected with a free, vagrant habit, although the flow of protoplasm and rhizopods is mainly from the 'dorsal' side, this also being the surface of temporary attachment. A second group, the Cibicidinae shows development of a flat or concave 'dorsal' attachment surface which becomes permanently attached and even embedded in various substrates (Haward and Haynes, 1976). Both groups showed considerable potential for further development. *Almaena* with basal median and marginal apertures developed from *Anomalinoides* in the Upper Eocene and *Anomalinella* with basal median and peripheral apertures in the Miocene. *Cibicides* shows a number of trends connected with attachment in the Tertiary, irregularly uncoiled biserial growth in the Eocene *(Dyocibicides),* irregularly uncoiled uniserial growth *(Rectocibicides)* and annular discoid growth (Annulocibicides) in the Miocene.

Cibicides also gave rise to the Planorbulinidae in the Eocene by assumption of rings of alternating chamberlets with peripheral apertures. Almost immediately, genera arose with thick secondary deposits of calcite on either side, or thick lamellae as in *Linderina* which shows incipient orbitoidal morphology.

The extraordinary, coloured, reefal Homotrematidae apparently arose from *Cibicides* in the Upper Cretaceous with the appearance of *Carpenteria. Rupertina* and *Biarritzina* are Eocene developments but the history of the modern genera *Homotrema* and *Miniacina* is still to be unravelled. The wild-growing and irregular Acervulinidae appear to have arisen from the Planorbulinidae, again in the Eocene.

The relationships of the Nonionacea are in dispute but the most primitive member of the Nonionidae appears to be *Nonionella,* Cret. – Rec., Jurassic records of *Nonion* being very doubtful. The umbilical lobe and ventral basal aperture in *Nonionella* are matched in certain families of the Discorbacea in which the umbilicus is secondarily closed. This appears to support Glaessner's idea of a close relationship between these groups and an origin within the Discorbacea, rather than the alternative suggestion that they sprang directly from the aragonitic Asymmetrinidae, or from the Robertinidae as suggested by Hofker. *Asymmetrina* has a crenulate, median aperture and the robertinids a complex partition. As discussed in chapter 11, it seems inherently improbable that relatively simple genera have arisen from complex end members of different wall structure groups.

Two evolutionary lines were established in the Cretaceous, apparently stemming from the trochospiral *Nonionella.* In both cases the trend was towards planispiral involute growth with low median aperture. In the Chilostomellidae the chambers are characteristically globular and few in number in each whorl, whereas in the Nonionidae the chambers remained relatively numerous and high with a tendency for the periphery to become angular and the umbilicus open or granulate. Both families remained hyaline oblique.

The work on the fine structure of the Elphidiidae, discussed in the previous section, supports the idea of a close relationship with the Nonionidae. Many features are gradational and the Nonionidae appear to have given rise to the Elphidiidae by progressive changes in wall structure, umbilical fillings and by bridging of excavated septal sutures (fissures) to give a canal system. The septal flap and canal system seem to be an independent development in this group (Haynes *et al.,* 1973; Hansen and Lykke-Anderson, 1976). But contrary views were expressed by Hofker, as already stated, who supposed that *Elphidium* has sprung from *Cushmanella* (Alliatinidae herein) and by Banner and Culver (1978) who suggest a polyphyletic origin for the family from within the Discorbacea, *Protelphidium* from *Gavelinella* (= *Brotzenella*) and *Haynesina* from *Aubignina.* An origin from *Cushmanella* seems unlikely considering the late appearance of this genus in the Tertiary and its aragonitic wall structure. *Protelphidium* and *Haynesina* seem closer to each other than to either of the discorbacean progenitors suggested. The immediate ancestor of *Protelphidium hofkeri* may be *Nonion applinae* which occurs at the same horizon in the Thanet Beds of Kent.

Protelphidium and *Elphidiella* appear in the Palaeocene and *Elphidium* with retral processes and partial septal flap in the Eocene. A return to trochospiral arrangement is seen both in *Polystomellina (= Notorotalia)* in the Eocene and in *Faujasina* which is restricted to the Pliocene. Uncoiling occurs only in the isolated case of *Ozawia,* in the Recent. So far, *Haynesina* has not been found in sediments older than Pliocene and Banner and Culver suggest it may have given rise directly to some of the simpler, Quaternary species of *Elphidium* which is thus considered polyphyletic.

STRATIGRAPHICAL USE OF THE SMALL ROTALIIDS

The small rotaliids become abundant in the Upper Cretaceous and rise to a dominant position among benthonic Foraminifera in the Cenozoic. Most families are established by the late Upper Cretaceous and all of them range down to the Recent. There are a number of genera of restricted range but application in biostratigraphy is mainly at the species level.

The rapid rise of the rotaliids in the Upper Cretaceous is emphasised by their rather meagre representation in the Lower Cretaceous. The list of index forms for the Lower Cretaceous prepared by Bartenstein (1979) reveals that of the 81 species and species groups selected, mostly nodosariids, robertinids and agglutinated forms, only 11 (12 per cent) are rotaliids. Of these, 7 belong to the *Gavelinella – Lingulogavelinella* gr. and the others are species of *Gavelinopsis, Valvulineria* and *Conorotalites.* These genera become valuable mainly in the late Lower Cretaceous, from the Hauterivian upwards and particularly in the Albian, especially species of the *Gavelinella – Lingulogavelinella* gr. (Scheibnerova, 1971a, 1971b; Price, 1976; Salaj, 1976). According to Price the *Gavelinella – Lingulogavelinella* plexus, including *L. albiensis,* is restricted to the Paris Basin in the Lower Albian but spreads widely in the Middle and Upper Albian. *L. albiensis* is then found in Britain and N.W. Germany and reaches 5 – 15 per cent of the total population in the Paris Basin. Salaj has shown that the Upper Hauterivian to Barremian interval is characterised by the evolutionary line *Lingulogavelinella sigmoicosta* to *L. barremiana* and the Aptian by the appearance of *L. agalarovae* and *L. complanata.* The Upper Barremian and Lower Aptian can also be dated by the evolutionary line *Conorotalites bartensteini bartensteini* to *C. bartensteini intercedens* to *C. bartensteini aptiensis.*

The *Gavelinella/Lingulogavelinella* gr. shares in the expansion of small rotaliids through the Upper Cretaceous, and Brotzen (1942) on the basis of borehole material was able to construct an evolutionary tree tracing three separate lines of evolution from the *G. intermedia* group in the Albian:

(1) Through *G. ammonoides* (Alb. – Tur.) to *G. costata* (Sen.) to *G. pertusa* (Maas) to *G. bullata* (Danian).
(2) Through *G. baltica* (Alb. – Tur.) to *G. cretacea* (Sen.).
(3) Through *G. moniliformis* (Alb. – Tur.) to *G. tumida* (Sen.) to *G. nelsoni* (Maas.).

Other genera of Cancrisidae such as *Gyroidina* and *Gyroidinoides* are now abundant, together with nonionaceans such as *Nonionella, Pullenia, Chilostomella* and *Allomorphina,* and Alabaminidae including *Alabamina* and *Osangularia.* The Anomalinidae are also much more important and include *Cibicides, Cibicidoides, Heterolepa* and *Stensioina.* As shown by Cita (1966) and Koch (1977), *Stensioina* has been found particularly valuable in correlation. The increased abundance of the small rotaliids by the late Cretaceous is well shown by the lists given by Surlyk and Birkelund (1977) for the Maastrichtian White Chalk in Denmark. These include: *Anomalinoides, Cibicides* (5 species), *Gavelinella, Osangularia, Pullenia* (2 species), *Rosalina* and *Stensioina.* However, despite this increase in abundance and their value in biostratigraphy they are still subordinate to other groups. This is shown by the lists given by Cushman (1946) for the Upper Cretaceous of the Gulf Coast region of the USA and adjacent regions where they make up only some 10 per cent of the 600 or so species recorded, the lists being heavily dominated by agglutinated genera, nodosariids and buliminids as well as planktonic genera.

In contrast to most groups of Larger Foraminifera, all the families of small rotaliids survived the environmental crisis brought about by the great end Maastrichtian regression and attendant palaeogeographical and climatic changes. *Gavelinella* was much reduced and *Stensioina* became extinct, but all the superfamilies show increased numbers and diversity through the Palaeocene with appearance of *Elphidiella, Laffiteina* and *Cycloloculina.* Small rotaliids now became one of the dominant benthonic groups. The Middle to Upper Palaeocene, Thanetian microfaunas of England are typical of this new aspect. Rotaliids are the dominant single group (approx. 33 per cent), together with nodosariids (especially polymorphinaceans), buliminids and rare robertinids and agglutinated forms. In absolute numbers of individuals they clearly dominate at most horizons. Members of the *Cibicides* group are most abundant and also strongly represented are *Anomalinoides, Asterigerinata, Gyroidinoides, Nonion, Nonionella, Protelphidium, Pullenia, Pulsiphonina* and *Rosalina.*

These small rotaliids are particularly important in Palaeocene biostratigraphy, not only because of the general absence of large rotaliids until the Upper Palaeocene but also because planktonic Foraminifera are small and lack diversity until the late Palaeocene. Furthermore, both large rotaliids and planktonics tend to be confined to low latitudes until the Eocene. They have therefore received detailed attention around the world since the pioneer studies of Koenen (1885) in Denmark, Burrows and Holland (1897) in Kent, England, and Bagg (1898) in New Jersey, USA; an added fillip being the importance of oil in the Lower Tertiary. Modern researches began with the classic work of Helen Plummer (1926) on the Midway of Texas and provide evidence of a microfauna with cosmopolitan distribution.

Further work in the European type area includes: North Sea Basin and Anglo-French – Belgian Basin (Franke, 1927; Staesche and Hiltermann, 1940; Ten Dam, 1944; Brotzen, 1948; Haynes, 1954 – 58; Rouvillois, 1960; Hofker, 1966; Kiessel, 1970; Gustafson and Norling, 1973; Fisher and Williams, 1975). This work has been carried into Poland (Pozaryska, 1965; Pozaryska and Szczechura, 1968) and into the Ukraine (Vasilenko, 1950; Kaptarenko-Chernoussova *et al.*, 1963; Kraeva and Zernetskii, 1969), the Crimea (Shutskaya, 1958, 1960; Morozova, 1960) and Tadzhikstan (Davidson and Morozova, 1964; Morozova *et al.*, 1965). Further work in the USA includes: the Gulf Coast region (Cushman and Ponton, 1932; Toulmin, 1941; Cushman, 1951; Kellough, 1959, 1965) and the Atlantic Coastal Plain of the USA (Jennings, 1936; Shifflett, 1948; McLean, 1951; Hofker, 1955; Page, 1959; Nogan, 1964). Investigation of the Palaeocene smaller benthonics has also been carried out in Egypt (Nakkady, 1950; Leroy, 1953), Libya (Berggren, 1974a), Tunisia (Aubert and Berggren, 1976), Algeria (Ten Dam and Sigal, 1950; Drooger, 1952a), Morocco (Rey, 1954) and in the Indian subcontinent (Haque, 1956). Other parts of the world where this interval has been studied include Greenland (Hansen, 1970b), S. America: Trinidad (Cushman and Renz, 1942), Argentina (Bertels, 1964, 1972; Malumian, 1970), and Australia (McGowran, 1965; Webb 1972, 1973). Very significant studies have also been carried out recently on the Palaeocene penetrated in JOIDES drill holes in the Atlantic: Rockall (Berggren, 1972a, 1974b; Murray, 1979), Norwegian Sea (Saito *et al.*, 1967) and Bay of Biscay (Schnitker, 1979).

The results of this intensive study carried out over a period of some four decades have been synthesised by Berggren and Aubert (1975). This reveals two main assemblages on muddy and silty substrates—a shallow, shelf fauna of 'Midway type' and a deep-water fauna of 'Velasco type', both with species that are largely 'amphi-Atlantic and Tethyan in distribution' and most of which range through the Palaeocene (Dano-Montian and Thanetian). A third, clear-water carbonate assemblage with high percentages of miliolids and *Rotalia* can also be distinguished. The Thanet fauna belongs to the 'Midway type' assemblage. Characteristic elements include:

Alabamina obtusa, midwayensis, westraliensis gr.
Anomalinoides acuta, midwayensis, nobilis, welleri.
Asterigerina aberystwythi, primaria gr.
Cibicidina mariae.
Cibicidoides alleni, proprius gr.
Gyroidinoides octoamerata, subangulata gr.
Protelphidium hofkeri.
Pulsiphonina prima.
Rosalina koeneni.
Rosalina ystadiensis.

These species occur with wide-ranging buliminids and uvigerinids including *Angulogerina europea* and the *Bulimina thanetensis, trigonalis* gr., large ornamented species of *Lenticulina, Astacolus, Vaginulina* and *Palmula* and the *Ceratobulimina perplexa, tuberculata* gr.

The deep-water 'Velasco type' assemblage is distinguished by greater prominence of *Gavelinella* and *Osangularia,* agglutinated genera and *Nuttallides* and *Nuttallinella* (resembling *Eponides* but with internal toothplates and placed in the Epistomariidae in the 'Treatise').

Berggren and Aubert conclude that the migration of the cosmopolitan species was accomplished by accidental 'waif dispersal' of juveniles put into suspension and transported by vertical and horizontal currents. The stratigraphical appearance of most species is regarded as simultaneous on both sides of the Atlantic. Tethys acted as a corridor for many species migrating from east to west, but the East Pacific apparently presented a major barrier.

During the Eocene the cyclic marine transgressions on to the continental areas typical of the Tertiary reached a maximum with consequent climatic optimum. Deep, cold-water circulation was not yet established in the Atlantic and subtropical conditions spread to high latitudes, including the British Isles area, then crossed by palaeolatitude 40°N (Berggren and Phillips, 1971). Conditions were very favourable for Foraminifera, especially along the east and west Tethyan 'corridor'. This is reflected in the appearance of new families such as the Planorbulinidae and Acervulinidae and the largest increment of new genera and species in the history of the small rotaliids: *Amphistegina, Asterigerina* s.s., *Astrononion, Cancris, Cribroeponides, Discorbis* s.s., *Dyocibicides, Elphidium, Florilus, Glabratella, Halkyardia, Melonis, Oridorsalis, Polystomellina, Siphonella* and *Siphonides,* among others.

The fauna of the latest Palaeocene (Sparnacian) is transitional and contains a mixture of species that range up from the Thanetian together with new forms. The new forms became dominant in the Lower Eocene, together with numerous later additional introductions, to produce a distinctive Eocene foraminiferal fauna. Many of the species continue through the late Palaeogene but the Oligocene is again characterised by new introductions, including new genera such as *Discorbitura* and *Parrellina.* The Palaeogene/Neogene boundary is marked by extinctions and by a second wave of new introductions in the Miocene including: *Anomalinella, Annulocibicides, Cellanthus, Cymbaloporetta, Cribroelphidium, Cribrononion, Poroeponides* and *Rectocibicides* among others. The assemblages are now increasingly dominated by species still extant, with *Faujasina* restricted to the Pliocene and *Hyalinea* to the Quaternary.

Many of these species are again cosmopolitan in distribution, particularly in the Palaeogene and early Miocene (Cushman, 1939; Martin, 1943; Gianotti, 1953; di Napoli Alliata, 1953; Ruscelli, 1953; Rey, 1954; Levin, 1957). As in the Palaeocene, two shelf assemblages can be distinguished, together with a deep-water assemblage with species first described from the Caribbean (Nuttall, 1932; Cushman and Stainforth, 1945; Beckmann, 1953). Cold, deep-water circulation was apparently established near the Eocene/Oligocene boundary, with the rise to abundance of pleurostomellids and stilostomellids (Berggren, 1972a; Douglas, 1973). The combined influence of the break-up of Tethys near the Oligocene/Miocene boundary and refrigeration of the polar regions from the late Miocene onwards appears to have led to increased provincialism. A definite cold-water (shelf) province becomes discernible in high latitudes in the late Neogene. Species typical of this cold-water assemblage, including *Hyalinea balthica,* penetrate the Mediterranean at the beginning of the Pleistocene (Bayliss, 1969). At the same time, bottom temperatures in the deep sea fell to present levels coincident with the appearance of the modern '*Cibicides wuellersdorfi* fauna'.

Work done on the classic Palaeogene section in the Anglo-French – Belgian Basin provides a good example of the application of the Smaller Foraminifera and, in particular, small rotaliids, in biostratigraphy and highlights some of the problems involved (Curry, 1966; Murray and Wright, 1974; Curry *et al.,* 1978). In part there is an inherent problem for zonal stratigraphy because of the way in which the series and stages were recognised in the first place and in the nature of the sediments. As many of the difficulties found in the attempt to apply molluscan distributions also apply to the benthonic forams, it is worth while to look briefly at the historical basis of Tertiary biostratigraphy. The foundations of Tertiary stratigraphy were laid by Lyell and Deshayes in the early nineteenth century. They were able to show that the Tertiary system could be subdivided according to the percentage of molluscan species still living. About 3.5 per cent of the total fauna recovered from the Lower Tertiary of the English and French sectors of the Basin were considered extant. This suggested the term Eocene, or dawn, of the Recent. On this basis the system was divided into four (Lyell, 1830–33):

Recent	50%, type section Italy.
Pliocene	35–50%, type section Italy.
Miocene	17%, type section Tourraine.
Eocene	3–4%, type section Anglo-French–Belgian Basin.

The wide separation of the series in different countries led inevitably to boundary problems and Beyrich (1854) grouped beds in Germany he thought younger than Eocene but older than Miocene into the Oligocene series. Meanwhile Lyell (1839) had split the Recent and erected the Pleistocene, in recognition of the glacial epoch. Finally, towards the end of the nineteenth century the lowest Eocene was recognised as a separate epoch (the Palaeocene) on the basis of floral differences (Schimper, 1874).

As time went on and identifications improved, the percentages were revised and it gradually became realised that very few Eocene and Oligocene species have actually survived until the present day. It is now recognised that by the late Tertiary the older Tertiary faunas had become almost entirely replaced. This has allowed the subdivision of the Tertiary into two subsystems: the Palaeogene (Palaeocene to Oligocene) dominated by extinct species and Neogene (Miocene and Pliocene) in which living species appear in abundance. The original, hoped for statistical basis for the recognition of the successive series of the Tertiary therefore did not materialise. However, it was soon found that the various formations contained characteristic molluscan assemblages (1800 species in the Paris Limestone alone). These, together with particular index species of short range, rapidly became the basis of the subdivision of the system and of the recognition of stages. When it was realised that the formations represented alternating periods of marine and continental sedimentation, the stages were equated with cycles of sedimentation (Rutot, 1883; Dudley Stamp, 1921), each cycle beginning with a marine transgression and ending with regression. Unfortunately, although cycles of sedimentation certainly took place (see below) this confused the rock units with the stages and led to overcomplication of the stratigraphy. It has since become apparent that the molluscan assemblages are facies faunas and that the ranges of the index forms also reflect environmental controls and tend to transgress the limits of the stages. For instance, although *Arctica morrisi, Pholodomya obliterata* and *Arctica scutellaria* succeed each other in the French Thanetian, they occur together in the Thanet Formation. These species disappeared with the onset of the marginal marine sedimentation of the Woolwich Facies, but both *A. morrisi* and *A. scutellaria* returned during the deposition of the London Clay. An even more serious difficulty is that a large element of the Eocene molluscan fauna is of subtropical to tropical origin. These species migrated into the Anglo-French–Belgian Basin from the Tethyan dispersal centre when conditions were favourable. As their ranges tend to be much longer in the Tethyan area this means that the zones that can be distinguished in N.W. Europe cannot be carried outside the region and are only of local significance.

More satisfactory regional and inter-regional correlation was achieved on the basis of the biozones of short-ranged Larger Foraminifera, in particular the nummulites, but here again, although *Nummulites* shows rapid evolution with complete lineages discernible in Tethys, the species only appear sporadically in the North-west European section. The typical Palaeocene species do not occur and only one species, known from Germany, occurs in the region in the Oligocene. However, although these species, like the mollusca, are clearly subject to environmental control their short biozones mean that their times of appearance and disappearance in the Basin provide valuable datum lines.

In contrast, the small Foraminifera occur in all the marine formations, often in considerable abundance. But apart from the recognition of the value of certain short-ranged species, no general zonal scheme has been erected on the basis of their distribution. This is because, like the molluscan species, many are of long range and the assemblages are largely facies faunas, often closely tied to substrate. However, as pointed out by Curry (1966) in the analogous case of the mollusca, the evolutionary studies necessary to delimit rational index forms in this group have hardly begun to be carried out. The accompanying chart (figure 12.2) is arranged to show how all the stages are distinguished by numerous first appearances as well as by restricted occurrences. Although some species, once they have made their entry, range through the Palaeogene or even, like *Cibicides lobatulus,* range down to the Recent, a number of species reach their acme in a particular zone or are confined to one or two stages only.

The chart brings out the general sequence of small rotaliid distribution discussed above. The Thanetian fauna includes restricted species but

EPOCH	SERIES	FORMATIONS STAGES	FORMATIONS TYPE	EQUIVALENTS		SMALLER FORAMINIFERA		LARGER FORAMINIFERA & (PLANKTON)	P	N
OLIGOCENE	UPPER	CHATTIAN	Cassel Sands	Beauce Ls Voort Sands		Almae. osnabrugensis Angul. gracilis Aster. gurichi^{+} Cancr. auriculus Cib. tenellus° Frond. oblonga Heter. dutemplei° Vagin. gladia		(Globigerina ciperoensis angustiumbilicata, ciperoensis angulisuturalis, opima opima; Globanomalina extinction).		
	MIDDLE	RUPELIAN	Boom Clays	Berg Sands, Septarion Clays, Fontainebleau Sands, Magdeburg Sands. U. Hampstead		Alab. perlata Alab. tangentialis Allom. macrostoma Aster. preplanorbis B. cookei Cycl. placenta	Epon. pygmaeus Epon. umbonatus Non. buxovillanum N. parvulum N. ella lobsannensis Valv. petrolei	(Wetzeliella gochtii, Globigerina oauchitaensis, ciperoensis, munda officinalis, oauchitaensis, prebulloides)	19 -	23 -
	LOWER	LATTORFIAN	Lattorf Sands	L. Hamstead Bembridge Ml Bembridge Ls Osborne U. M. Headon	Brie Ls/ Gyp. Mls Sannois Green Clays of Romainville Tongeren, Grimmertingen Sands	Alab. wolterstorffi Aster. bartoniana° Bol. beyrichi gr. B. oligocaenica Cauc. coprolithoides Cancr. turgidus Disc. kiliani Non. granosum	Prot. cf. roemeri Par. curryi° Quinq. contorta° Quinq. reicheli° Ros. douvillei Turr. acicula T. alsatica	Nummulites germanicus (? prestwichianus extinction) (Ericsonia subdistichia Globigerina tapuriensis)	18	22 21
EOCENE	UPPER	LUDIAN	Champigny Ls/ Montmartre Gyp. Ph. ludensis marls	L. Barton Sands Barton Clay	Asse Sands Asse Clays	Aster. bartoniana Cib. pseudoungerianus Epist. oveyi Epon. candidulus Elph. latidorsatum E. minutum	E. subnodosum Fabul. bella Gland. laevigata Halk. minima^{+} Heter. dutemplei Par. subinermis	Num. orbignyi Num. prestwichianus Num. variolarius (extinction) (Globigerinatheka index Wet. perforata, draco)	17 to 12	20 to 16
		LEDIAN	Sands of Lede	U. Sands of Beauchamp	Wemmel Sands					

EOCENE	MIDDLE	LUTETIAN	Gr. Paris Ls (U) Gr. Paris Ls	Bracklesham Group L.	Brussels Sands	Aster. campanella$^+$ Bol. eocenica B. parisiensis Cyloc. eocenica Disc. vesicularis$^+$ D. propinqua Fabul. discolithes$^+$	Lind. brugesi Melon. affine Para. inermis Ros. bractifera Rot. trochidiformis Quinq. reicheli Q. simplex	Alveol. elongata$^+$ Orbit. complanatus, Alv. boscii$^+$, Num. laevigatus,$^+$ variolarius, Num. lamarcki$^+$ (also Globor. bullbrooki, Trunc. rohri, T. spinuloin-inflata. Wet. coleothrypta)$^\circ$	11 to 10	15 to 14
	LOWER	CUISIAN	Cuise Sands	Bagshot Beds Claygate U. M. L. London Clay	Belleu Ls Panisel U. M. L. Flanders Clay	Alab. westraliensis Canc. subconicus Cib. lobatulus C. mauricensis C. producta Epon. polygonus	Glabr. herouvalensis Gyroid. magna Par. curryi P. spinigera Plan. burlingtonensis	Num. planulatus$^+$ Alveolines of oblonga gr.$^+$ (also Glob. aquiensis, yeguaensis, Globrot. sub-botinae; Trunc. (Acar.) esnaensis, pentacamerata, perclara; Globanomalina sp. Wet. varielongituda, Wet. similis, Discoaster hibrachiatus)	9 to 6a	13 to 10
PALAEOCENE	UPPER	SPARNACIAN	Ostrea Clays Sinceny Sands Lignites and Plastic Clays Meudon Congl.	Blackheath Woolwich & Reading, Landen fluvio marine facies		Mixed assemblage of 'Midway type' and newforms. Angul. muralis Aster. guerri Bol. adamsi Cib. tallahatensis C. westi Elph. hiltermanni		(Wet. meckelfeldensis Wet. hypercantha First appearance of Wetzeliella)	5	9
	MIDDLE	THANETIAN	Thanet	Bracheux Sands Ostend Sands, Sands of Rilly, Greensands of Lille and Hainout, Marls of Gelinden, Cernay conglom.		Alab. obtusa$^\circ$ Ang. europea$^\circ$ Anom. nobilis$^\circ$ Aster. aberystwythi$^+$ Astac. platypleura$^+$ Cib. cunobelini$^\circ$	Cib. cunobelini$^\circ$ C. mariae$^\circ$ C. succedens$^\circ$ Cib. proprius$^\circ$ Epon. toulmini Prot. hofkeri$^\circ$	(Heliolithus riedeli Discoaster gemmeus)	4	8 to 7

Species are first occurrences except where marked: restricted$^+$ acme$^\circ$

Figure 12.2 Chart showing first appearance of important smaller benthonic species in the Palaeogene of the Anglo-French – Belgian Basin. Data from Batjes (1958), Kaasschieter (1960), Bramlette and Sullivan (1961), Hay *et al.* (1967), Yolande Lecalvez (1970), Murray and Wright (1974), Lucy Costa *et al.* (1976), Banner (1977). N.B. **Precise limits of Planktonic Foram Zones (P) and Nannoplankton Zones (N) not yet established. *Asterigerina* is used in the wide sense to include *Asterigerinata***

others such as *Alabamina obtusa, Cibicidina cunobelini* and *Cibicidoides proprius* range into the Sparnacian. Here they are joined by species such as *Cibicides tallahatensis, C. westi* and *Elphidium hiltermanni* which range up into the Eocene or even Oligocene. The new fauna becomes dominant in the Lower Eocene and this stage (Cuisian) is also distinguished by the first appearance of Larger Foraminifera in the Basin together with planktonic Foraminifera. Very large numbers of new species appear in the Lutetian (only a selection is listed) and there is a further increment in the Upper Eocene. The first appearances of distinctive new species also distinguish the Oligocene, with overlap of species from the Eocene, particularly noticeable in the Lower Oligocene, and appearance of species that become abundant in the Miocene, especially noticeable in the Upper Oligocene.

Although much more work has to be done to establish how many of these first occurrences are true evolutionary events and despite the complication caused by the co-existence in the Basin of both the muddy silt and clear-water sand facies, well marked from the Lutetian onwards, some groups do appear to be of particular value. As pointed out by Yolande Lecalvez (1970) these show the following possible evolutionary lines: from *Protelphidium hofkeri* (Thanetian), *Elphidium laeve* (Sparnacian) to *E. minutum* and *E. subnodosum* in the Bartonian; from *Asterigerina aberystwythi* (Thanetian) to *A. guerrae* (Sparnacian) and possible links with *A. bartoniana* (Bartonian), *A. dollfussi* (L/M Oligocene) and *A. gurichi* (U. Oligocene 'Asterigerina Zone'); from *Pararotalia spinigera* to *P. curryi* (Cuisian) to *P. inermis* (Lutetian) to *P. subinermis* (Bartonian). A possible evolutionary line in the Buliminida is *Angulogenerina europea* (Thanetian) to *A. muralis* (Sparnacian). As can be seen from the chart, other groups worth further study are the species of *Alabamina, Cancris* and *Rosalina*.

The difficulty experienced by earlier workers in correlating the North-west European stages with those recognised in other regions has now been much alleviated. First, by the discovery of planktonic Foraminifera in much greater abundance than had been thought (Drooger and Batjes, 1959; Berggren, 1969a, 1971; Bignot and Lecalvez, 1969; Marks and Vessem, 1971; Wright, 1972; Murray and Wright, 1974), and secondly by the use of nannoplankton (Bramlette and Sullivan, 1961; Hay *et al.*, 1967; Martini and Moorkens, 1969; Martini, 1970a, 1970b; Costa and Downie, 1976; Lucy Costa *et al.*, 1976). As shown by the chart these discoveries considerably supplement the Larger Foraminifera, although the precise limits of the planktonic zones are still to be worked out. There seems little doubt that further work will improve the correlations and obviate the supposed need for substitute type sections, although great care has to be taken to eliminate resistant reworked specimens.

Despite this advance, fierce controversy still rages over the boundaries of the Eocene and the status and limits of the Oligocene stages. To some extent this is a matter of definition and semantics but confusion has been caused by the attempts of some workers to redraw the boundaries in ways which effectively exclude the classical type sections. This follows, in particular, if emphasis is put upon the mammal faunas which automatically shifts the boundaries from the base of the marine formations to horizons representing the culmination of the regressions, a procedure which offends stratigraphical practice and is justly criticised by Curry (1966).

In recent French studies (Feugueur 1955; Blondeau *et al.*, 1965; Curry *et al.*, 1969; Lecalvez, 1970) the Sparnacian, including the Woolwich and Reading Beds, is placed in the Lower Eocene. This move is supported by the difference in the vertebrate faunas of the Cernay Conglomerate of Rheims (Thanetian) and the Woolwich Bottom Bed (Gurr, 1962; Russell, 1964). The Woolwich and Reading Beds are therefore considered younger than the fluvio-marine Landenian of Belgium. However, as Schimper (1874) originally based the Palaeocene upon the Sparnacian, it is clear that this stage should not be removed to the Eocene unless there are compelling reasons for such a drastic course of action. Fortunately the weight of evidence appears to be on the other side.

First, the Thanet Formation has been correlated with the zones of *Globorotalia pusilla* and *G. pseudomenardii* (Globigerinacean zones P3 and P4) by indirect reference to the contained nannoflora which includes *Discoaster gemmeus* and *Heliolithus reideli* (Bramlette and Sullivan, 1961; Luterbacher and Premoli Silva, 1964; Hay *et al.*, 1967; Banner, 1977). Thus, following Samanta (1974) the Thanetian is Middle and Lower, Upper Palaeocene in age. Removal of the Woolwich and Reading Beds to the Lower Eocene (Globigerinacean zones P6 – 9) thus predicates an hiatus equivalent to the *G. velascoensis* zone (P5), recognised as Upper Palaeocene throughout the world. At the type section (Reculvers, Herne Bay, Kent) the Woolwich Bottom Bed follows the Reculver Silts disconformably, but with no evidence of a prolonged break of some 2 million years duration.

Secondly, as has been noted above, both the Lower London Clay and the Sands of Sinceny contain a mixed assemblage of small rotaliids of 'Midway type' plus new species. The new species become dominant coincidently with the influx of the planktonics of the *G. subbotinae* zone (P6) and the appearance of *Nummulites planulatus* at the beginning of the Cuisian (Murray and West, 1974).

Thirdly, the dinoflagellate work of Lucy Costa and Downie (1976) indicates that the Woolwich and Reading Beds and the Landenian of Belgium are coeval, both belonging to the Wetzeliella hypercantha zone. The appearance of *W. similis* also conveniently coincides with the beginning of the Cuisian. It is therefore logical to draw the Eocene boundary at this horizon.

Similar attempts to extend the Eocene have been made at the top of the section, the boundary being moved up to encompass strata, hitherto included in the Lattorfian, on the basis of Mollusca (Krutzsch and Lotsch, 1964) and mammals (Blondeau *et al.*, 1965). This can also be rejected as undesirable on the grounds that the Oligocene was defined on the basis of these beds in the first place. Nevertheless, Curry *et al.* (1969) also include the Middle and Upper Headon Beds and the correlative Grimmertingen Sands in the Eocene on the evidence of mammals and charophytes, and the Sannoisian is made a substage of the Stampian s.l. In contrast, Denizot (1968) brings the Oligocene boundary down to include all the Ludian except the Pholodomya ludensis Marls and recognises a Lower Tongrian (Montmartre substage) and Upper Tongrian (Sannoisian substage).

In the face of these contradictions, the traditional tripartite stage division for the Oligocene is retained on the chart. Further work will show whether these divisions are more than zones (or even facies) of a single stage and sedimentary cycle, as postulated by Berggren (1971). Certainly the three divisions appear recognisable from the foraminiferal faunas.

ECOLOGY

At the present time the small rotaliids occur widely across the shelf down on to the abyssal plain (Norton, 1930; Phleger, 1960; Murray, 1973b) but they are especially characteristic of the shallow shelf. As mentioned earlier, this successful adaptation to life in high energy environments is shown by the high proportion of trochospiral tests (>50 per cent), the limpet-like, planoconvex test being perfectly fitted to fixed or temporarily attached life on weed or hard substrates. Biconvex trochospiral genera and planispiral forms (17 per cent) occur as mobile vagrants, again clinging by their pseudopods in weed or on the less disturbed sedimentary substrates.

Observations by Banner (1978) indicate the usefulness of trochospiral biconvexity combined with a keeled periphery in *Amphistegina lessonii.* This species is very mobile, travelling up to 3 cm a day in a petri-dish with its keeled margin raised above the substrate. The pseudopods not only spread out from the aperture on the ventral side but from the keel like a spider's web, by this means creating a net to entangle small arthropods. Pustules on the ventral surface (as in *Asterigerina)* channel the food particles and aid in physical disaggregation.

The dominant families of the inner shelf are the Elphidiidae *(Elphidium* and *Protelphidium),* the Discorbidae *(Discorbis* and *Rosalina),* the Asterigerinidae *(Asterigerina* and *Amphistegina),* the Nonionidae *(Nonion* and *Nonionella),* the Anomalinidae *(Cibicides)* and the Planorbulinidae *(Planorbulina). Elphidium* is particularly abundant in the marginal marine and turbulent zone (Parker, 1948) with keeled species in normal marine environments and species with rounded peripheries in the muds of brackish (hyposaline) marshes (Murray, 1968, 1973b). Two main facies can be distinguished in inner to midshelf, normal marine to slightly hyposaline environments, as found by Lowman (1949, 1951). A muddy sand or silt facies dominated by *Cibicides* with *Nonionella* and *Protelphidium,* typified by the western Gulf of Mexico, and a clear-water, shell sand facies dominated by *Asterigerina* and *Amphistegina,* as typified by the eastern Gulf of Mexico. Hypersaline environments tend to be dominated by miliolids but with the Asterigerinidae, Elphidiidae and large rotaliids next in abundance—see chapter 8. It is noteworthy that in the area of the Florida – Bahamas Platform, *Amphistegina lessonii* and *Rosalina rosacea* show a marked preference for areas of reef growth. Species with sharp peripheries are localised at the platform margin, including *A. lessonii, Asterigerina carinata, R. rosacea, Eponides antillarum* and *Poroeponides lateralis.* This also includes red-shelled species such as *R. rosacea* (? produced by former presence of zoozanthellae). *A. lessonii, E. antillarum* and *P. lateralis* are also typical of the shallow, open marine, seaward edge of the platform (Rose and Lidz, 1977).

The characteristic rotaliid families of outer shelf and bathyal environments are the Cancrisidae *(Cancris, Gyroidina, Gyroidinoides* and *Valvulineria),* Chilostomellidae *(Allomorphina, Chilostomella* and *Pullenia),* Alabaminidae *(Alabamina, Osangularia),* Nonionidae *(Nonionella, Melonis)* and Anomalinidae *(Cibicidoides, Planulina* and *Hyalinea).* As recognised by Bandy (1960a) these families, like the Buliminida discussed earlier, show important morphological trends when traced from the shelf to deeper waters. Compressed species of *Pullenia* occur on the shelf while globose species are characteristic of the bathyal zone. Again, sharp-edged members of the Cancrisidae *(Cancris)* occur on the shelf while rounded, globose species of *Valvulineria* and *Gyroidina* occur on the slope and in the abyss. This general trend to a rounded, biconvex form is consistent with a mobile habit on, and partially in, soft muds of the deep sea bed. Members of the agglutinated group, including *Trochammina* and *Haplophragmoides,* show similar trends.

The pattern of distribution of the families of small rotaliids evident in the Recent is already discernible to some degree by the late Cretaceous. Indeed, Sliter (1972) and Sliter and Baker (1972) go so far as to assume that Cretaceous benthonic assemblages occupied depth habitats similar to modern assemblages to depths of at least 2000 m. This means that the genera of the Alabaminidae, Cancrisidae and Chilostomellidae which appear in the early Senonian are taken to be indicative of outer shelf and slope depths at that time in the Pacific and Atlantic.

During the Tertiary, with the appearance of many new genera, there is a much closer approximation to the modern pattern which has thus been used extensively as a model for palaeoecological interpretation. Good examples are the work of Lowman (1949), Kellough (1959, 1965), and Tipsword *et al.* (1966) in the Gulf Coast of the USA, Youssefnia (1978) on the Atlantic Coastal Plain, USA and Bandy and Kolpack (1963) in California. However, it must be emphasised that comparisons based on species distributions are not effective beyond the Miocene and cannot be made at all in the early Palaeogene. It must also be stressed that, as in the case of the agglutinated group, discussed in chapter 6, the student must avoid applying Recent 'depth ranking' uncritically to the past. For instance, although many deep-water species apparently have consistent upper depth limits over wide areas (Bandy, 1954; Bandy and Arnal, 1957; Phleger, 1960, 1964; Smith, 1964) these ranges are only indirectly related to depth. Thus, Pearce (1980) has been able to demonstrate that the depth zones distinguishable in Rockall Trough, N.E. Atlantic, are in large part related to the change over from arenaceous to 'Globigerina' ooze substrates down the Continental Slope and to the gradual fall in temperature to uniformly low values on the Abyssal Plain. Significantly, *Cibicides wuellersdorfi,* which is confined to abyssal depths in the Rockall Trough, ranges up to bathyal depths in the cold (sub-zero) Norwegian Sea Water of the Faroes – Shetland Channel. Similarly, *Cibicides refulgens,* found only in the Upper Bathyal Zone elsewhere, ranges down to the Lower Bathyal Zone on the Wyville – Thomson Ridge where hard, current-swept substrates exist at great depths. Clearly, species will extend their 'depth ranges' when particular environmental factors allow. It is therefore not surprising that Streeter (1973) and Schnitker (1974b) found evidence for marked shifts in benthic foraminiferal faunas in the N. Atlantic during the Pleistocene which could not be simply related to depth control, and that categories as broad as the genus have been found to have different depth ranges in the Palaeocene by Youssefnia (1978).

The problems encountered in stratigraphical correlation of the Palaeogene of the Anglo-French – Belgian Basin have already been discussed in some detail; it is therefore appropriate to look at attempts to interpret the environmental significance of the faunas in this region also. This gives us the chance to look at the application of certain statistical measures that have been developed in a simplified and elegant way by Murray (1968, 1973b).

During the early Tertiary the Anglo-French – Belgian Basin was an extension of an enlarged North Sea Basin, largely closed off to the south-west except for intermittent connections with the Western Atlantic and Aquitaine via straits in the Start Point – Cherbourg Ridge. Uplift along the Weald – Artois line from S.E. England to Belgium, with the creation of the 'Wealden Island', also hindered communication. The basin was a restricted part of a much larger basin that was also largely enclosed, except to the north and connected only by narrow straits across Poland to Eastern Tethys and the East European Basin (Pozaryska, 1978)—see figure 12.3.

The Anglo-French – Belgian Basin became filled with deltaic and shallow marine sediments during the Palaeogene, brought in by a system of rivers that can already be referred to as the proto-Thames, the proto-Seine and the proto-Rhine. A maximum of some 600 m of sediments

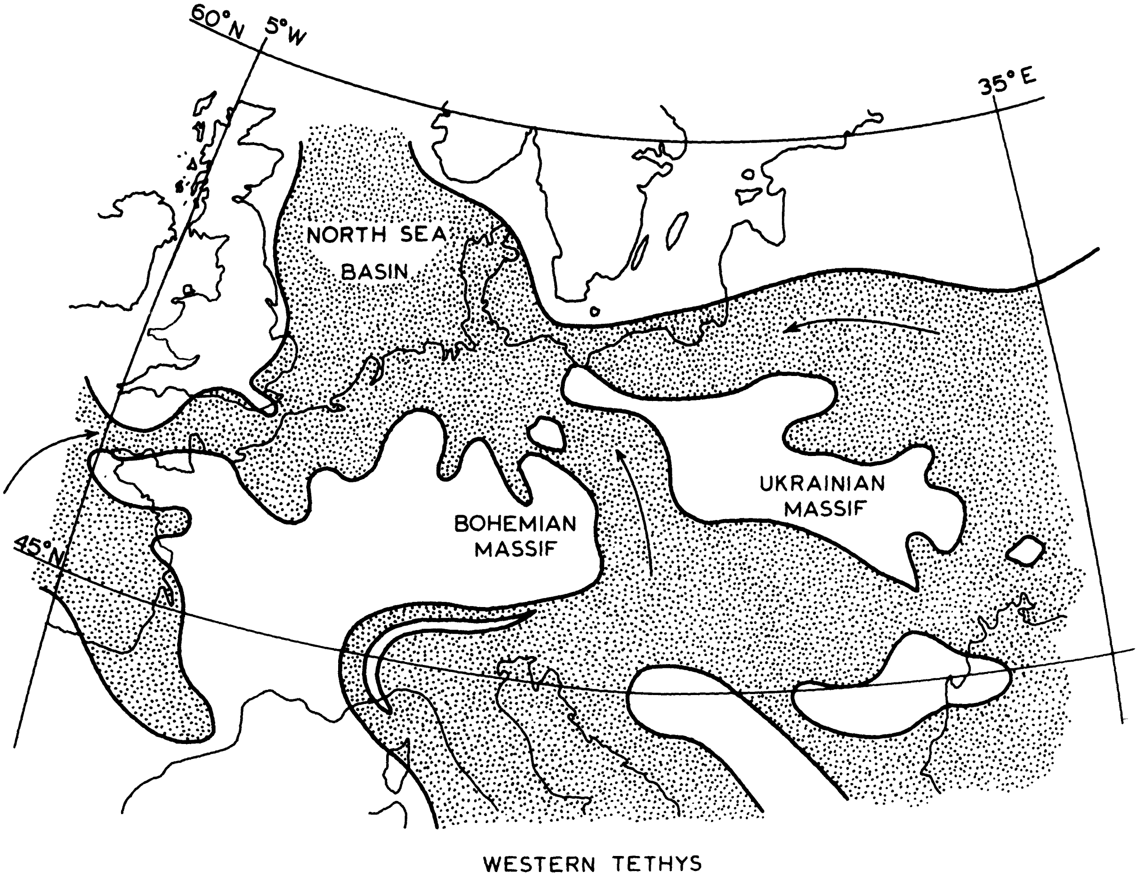
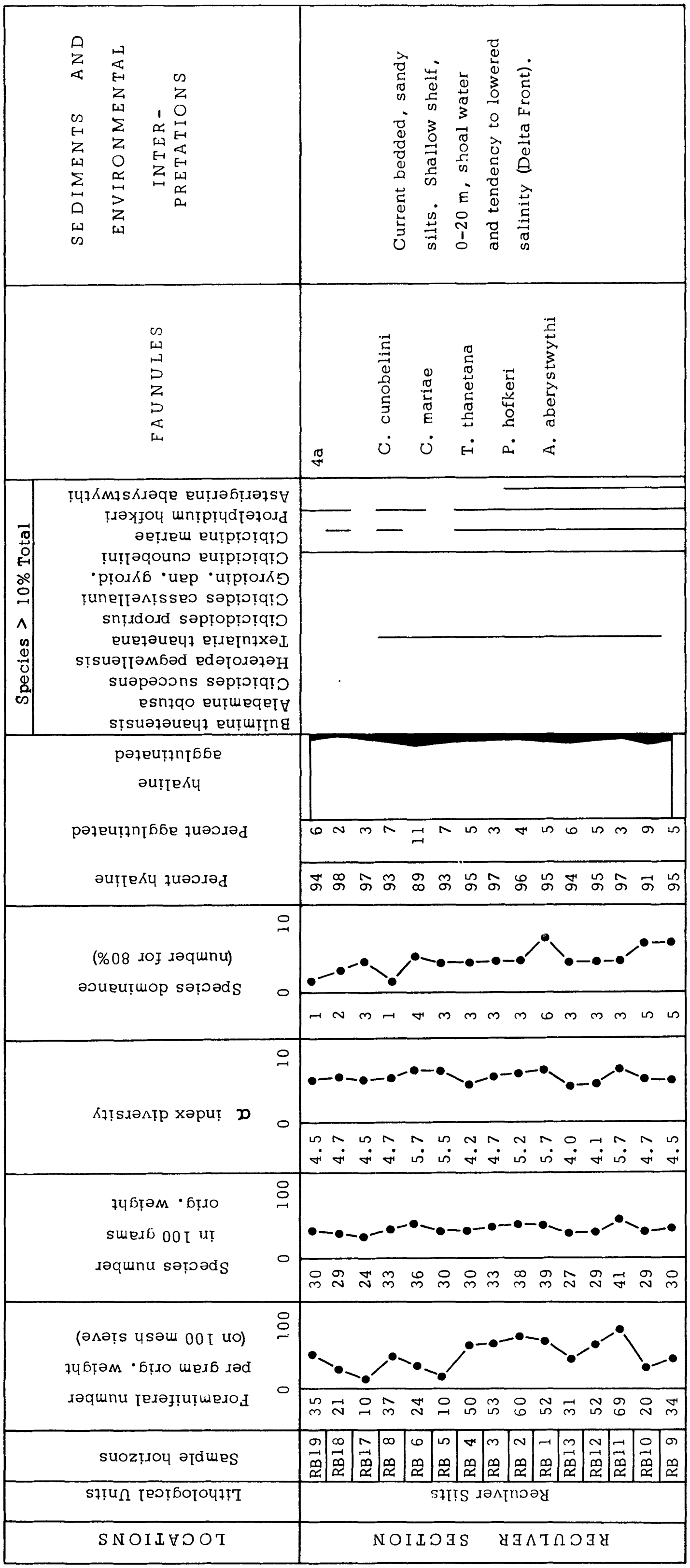


Figure 12.3 Map showing the N.W. European Basin and its connections during the Upper Eocene; faunal migration routes shown by arrows. After Krystyna Pozaryska (1978)

accumulated in the English sector. As has been discussed earlier, sedimentation was strongly cyclical, and well-marked transgressive and regressive phases can be distinguished. The foraminiferal faunas show a close relationship to the sedimentary facies and thus to the successive advances and retreats of the sea (Bhatia, 1957; Haynes, 1958c; Wright and Murray, 1972; Murray and Wright, 1974). However, there are complications in that not only are the three main shallow shelf benthic facies well marked by the Palaeocene, as already mentioned in the biostratigraphical section, but also the tendency towards restricted circulation led to stagnant bottom conditions from time to time. This means that the distributions cannot be interpreted as simple, straightforward indications of temperature and depth.

The dominance of small rotaliids (plus *Rotalia* and *Pararotalia*) in the microfaunas is well shown by the percentages given by Yolande Lecalvez (1970) for the Paris sector. These reveal total dominance of the muddy silt facies in the Palaeocene with 85 per cent small rotaliids and no miliolids. Miliolids only appear in appreciable numbers in the clean shell sand and the hypersaline carbonate facies and are dominant only in the upper part of the Middle Eocene, the lower part of the Upper Eocene and in the Lower Oligocene.

It is instructive to look in more detail at distribution charts prepared for the Palaeocene and Lower Eocene of the English sector (figures 12.4 and 12.5). Figure 12.4 is a reinterpretation of the data from the type sections of the Thanet Formation, employing methods adopted by Murray and Wright (1974), as shown in their interpretation of the London Clay of Whitecliff Bay, Isle of Wight (figure 12.5). This involves measuring, in particular, faunal dominance, diversity and the percentage of wall structure groups. It resembles Johnson's approach to palaeo-ecological analysis discussed in chapter 9, but makes use of the Fisher alpha index of diversity which allows the possible environment of deposition to be read off a summary chart



LOCATIONS	Lithological Units	Sample horizons	Foraminiferal number per gram orig. weight (on 100 mesh sieve)	Species number in 100 grams orig. weight	α index diversity	Species dominance (number for 80%)	Percent hyaline	Percent agglutinated
RECULVER SECTION	Reculver Silts	RB19	35	30	4.5	1	94	6
		RB18	21	29	4.7	2	98	2
		RB17	10	24	4.5	3	97	3
		RB 8	37	33	4.7	1	93	7
		RB 6	24	36	5.7	4	89	11
		RB 5	10	30	5.5	3	93	7
		RB 4	50	30	4.2	3	95	5
		RB 3	53	33	4.7	3	97	3
		RB 2	60	38	5.2	3	96	4
		RB 1	52	39	5.7	6	95	5
		RB13	31	27	4.0	3	94	6
		RB12	52	29	4.1	3	95	5
		RB11	69	41	5.7	3	97	3
		RB10	20	29	4.7	5	91	9
		RB 9	34	30	4.5	5	95	5

FAUNULES

4a

C. cunobelini

C. mariae

T. thanetana

P. hofkeri

A. aberystwythi

SEDIMENTS AND ENVIRONMENTAL INTER-PRETATIONS

Current bedded, sandy silts. Shallow shelf, 0-20 m, shoal water and tendency to lowered salinity (Delta Front).

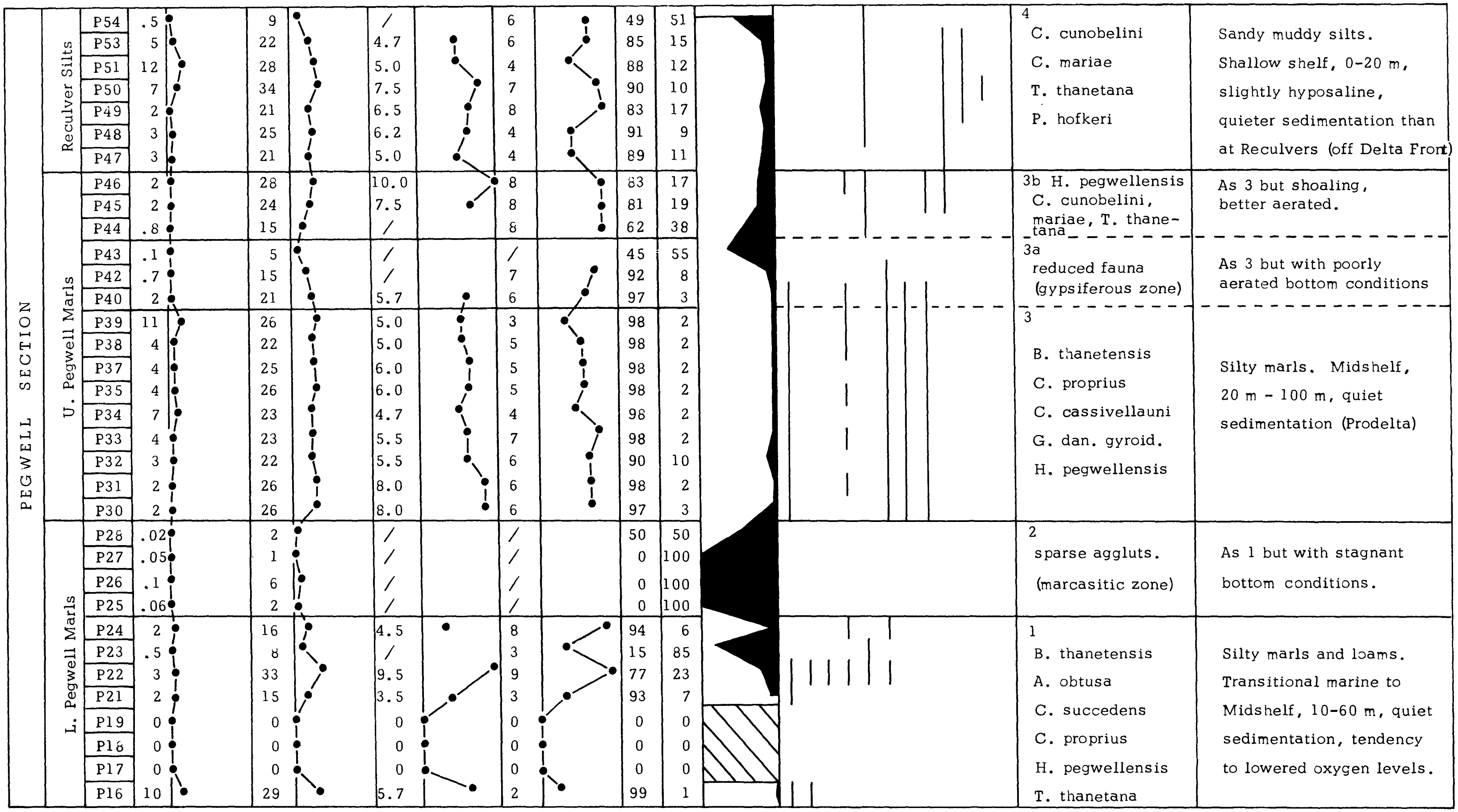


Figure 12.4 General features of the foraminiferal assemblages (dominantly small rotaliids) in the Thanet Formation of Kent, and an environmental interpretation

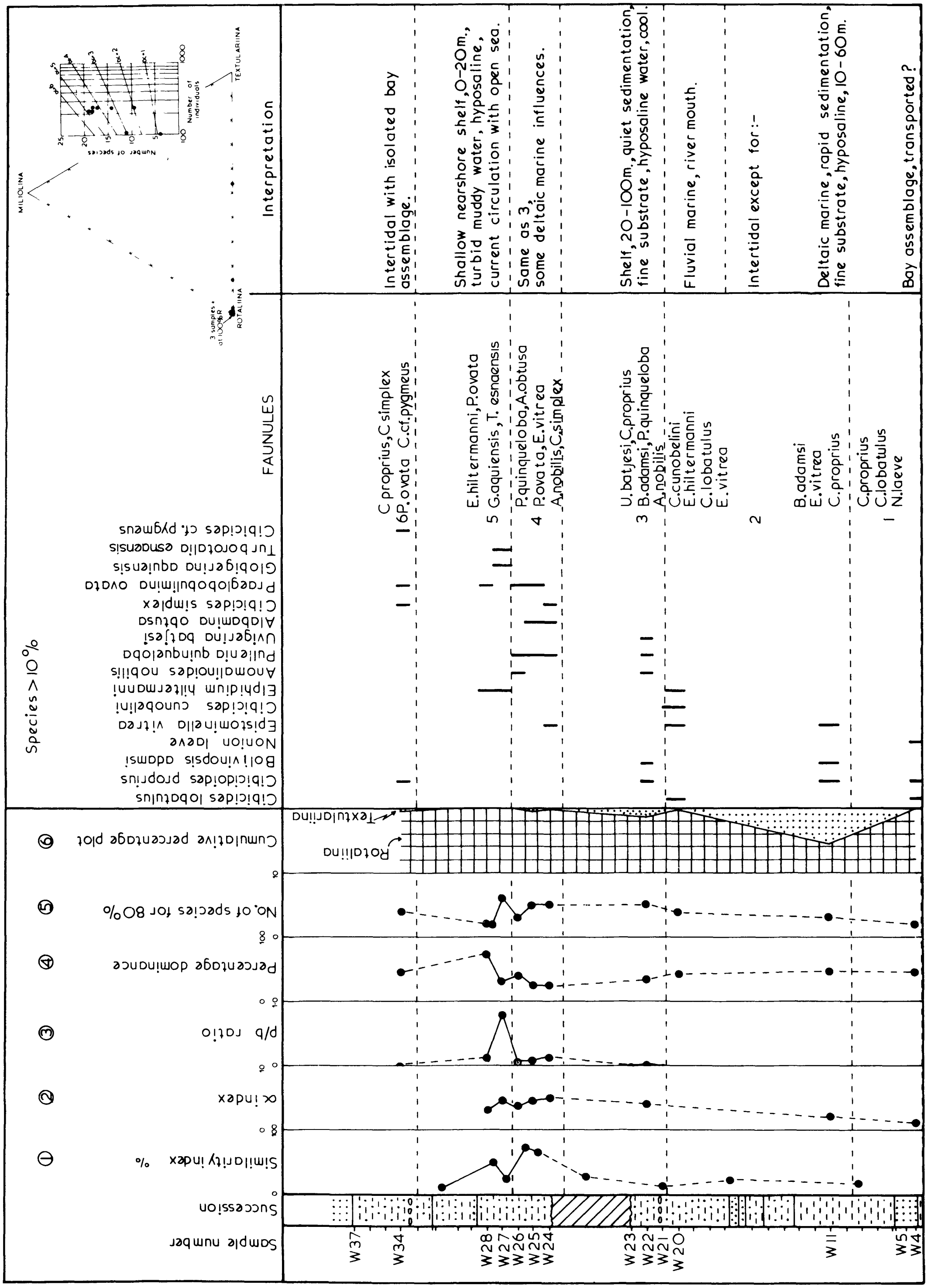


Figure 12.5 General features of the foraminiferal assemblages of the London Clay, Whitecliff Bay, Isle of Wight, and an environmental interpretation. From Murray and Wright (1974)

(Murray, 1973b, figure 101) and combined with information obtained by plotting the percentage of the three major wall structures on a triangular diagram (Murray, 1973b, figure 102).

The percentages of major wall structure groups are roughly similar in the two formations with hyaline calcareous forms dominant, agglutinated forms subordinate and porcelaneous forms absent. The London Clay samples plot in the hyaline (Rotaliina) corner and on the base line of the triangle (figure 12.5). The Thanet samples are not plotted in this way but would occupy the same position, with three in the agglutinated (Textulariina) corner. This is a general indication of shelf seas or hyposaline marshes.

Diversities are low in the London Clay. As shown by the graph and the plot in the right-hand corner of the figure, they do not exceed 5 and can be interpreted as hyposaline, nearshore shelf. In the Thanet Formation, in contrast, the lowest value is 3.5 and almost two-thirds of the 37 samples measured reach 5 or more, rising to a maximum of 10. These figures indicate shelf seas in which normal salinities generally prevailed.

As can be seen from the lists of species (>10 per cent of the total for each sample) both formations tend to be dominated by *Cibicides* and thus belong to the muddy silt, shallow shelf facies. The differences in salinities can be explained by the location of the Thanet sections, on the North Sea side of the Wealden 'island' or peninsula and further from the delta front, except at the close of the marine phase.

The figures for dominance agree with the salinity interpretation. Dominance is generally strong in the London Clay and the values rise to 5 and above only in Faunules 3, 4 and 5 (figure 12.5). In the Thanet Formation it is weaker and values up to 9 occur in the Pegwell Marls, but low values are shown by the Reculver Silts at Reculver.

The planktonic/benthonic ratio is out of key in that it is not measurable in the Thanet Beds. Greater abundance of the planktonics in the London Clay is probably connected with the brief opening of the Western Approaches at the acme of the London Clay transgression.

Foram number and species numbers are plotted for the Thanet Beds and are roughly correlated, reaching a maximum in the Reculver Silts. Imperfect correlation, especially in the Silts, is probably a result of current mixing and winnowing. As is to be expected, there is a general correlation between species number, dominance and the alpha index.

As shown by figure 12.4, four faunules and three subsidiary units are recognised in the Thanet Formation. Faunule 1 shows sedimentation under rapidly fluctuating conditions, indicated by the highly variable values of all the measurements, together with an extensive barren zone. Some of the highest values recorded throughout occur at P22, where dominance is 9 and species number 33, and also in P16, but here the extreme relative abundance of *Alabamina obtusa* and *Bulimina thanetensis* gives a dominance of 2, although species number is 29. The proportion of agglutinated species tends to be high and reaches 85 per cent in P23.

Although Ten Dam (1944) found the characteristic members of this faunule in beds intercalated with continental and brackish water beds in the Netherlands, there is an absence of specific brackish water indicators. Indeed, the presence of many species of nodosariids together with genera such as *Alabamina, Gyroidinoides, Pullenia* and *Cyclammina* could be taken as indicative of deep-water conditions. The fauna is therefore taken to indicate transitional marine to midshelf environments with a strong tendency to poorly aerated bottom conditions, sufficient to exclude the microfauna entirely through P17 – 19. Similar conditions probably also operated to exclude the faunas from the underlying, Stourmouth Clays (not shown on chart).

Faunule 2 is interpreted as reflecting prolonged stagnant conditions but with sufficient aeration to allow the existence of a sparse agglutinated fauna. However, it is possible that there was a calcareous element in the life assemblage as a number of casts of *Praeglobobulimina,* composed of minute pyrite balls, occur in equivalent inland sections (Haynes, 1958c). Nevertheless, agglutinated species reach their maximum number in this interval—ten in all.

Faunule 3 is taken to represent the establishment of normal midshelf sedimentation. The statistics indicate a fairly stable environment: average Alpha index = 6.5, Foram number = 6, Species number = 24, Dominance = 5 and low agglutinated percentage, although the alpha index falls below 5 at P34, and to 5 only at the top. This seems to herald the poorly aerated conditions thought responsible for the reduced fauna of Faunule 3a. The rise in the percent of agglutinated forms possibly indicates reducing conditions below the sediment/water interface, with formation of hydrogen sulphide and destruction of calcite tests to form selenite.

Faunule 3b exhibits the highest alpha index for any sample, = 10, and low dominance, a constant figure of 8. This can be explained as due to shallowing and better aeration brought about by the approach of the Delta Front with the first appearance of *Cibicidina cunobelini* and *C. mariae* to give a diverse, mixed fauna.

Faunule 4 represents the Reculver Silts at Pegwell. Foram number is low, average = 5, and species number = 23, actually both slightly lower than in Faunule 3. The alpha index is generally 5 or above but falls below 5 at the top. Dominance, average 6, is also slightly less than in Faunule 3. This faunule, high in *Cibicidina,* with *Protelphidium* and *Asterigerina,* is interpreted as shallow shelf with strong deltaic influences but off the Delta Front.

Faunule 4b represents the Reculver Silts at Reculvers. Although the dominant species are the same, there are marked differences. The Foram number 10 – 69, and species number 24 – 41 are very high but the alpha index is fairly constant between 4.2 and 5.7, average 4.7. Species dominance is also marked, average 3, and reaches 1 at RB8 and RB19 at the top of the section. This fauna is taken to represent hyposaline, Delta Front, conditions.

The London Clay shows much stronger deltaic influences throughout and Murray and Wright recognise six faunules which indicate the following succession of environments:

(1) At the base, intertidal conditions bordering a restricted bay and river outlet.

(2) Fluvial marine conditions in the mouth of a river channel.

(3) Shelf, quiet sedimentation, clay substrate, 20 – 100 m depth, hyposaline water, removed from river mouth.

(4) Shallow nearshore shelf, 0 – 20 m, good current circulation.

(5) Intertidal conditions.

The results of these analyses demonstrate the usefulness of the statistical measures. There is clear evidence of a marine cycle in the London Clay from intertidal through open marine back to intertidal conditions, and in the case of the Thanet Formation support is given to the idea (Haynes, 1958c) that the Pegwell Marls represent the transgressive phase and the Reculver Silts the beginning of the regressive phase. But the statistics allow much greater precision and detail in the

AGE	Core Nos.	Depth (m.)	Characteristic foraminiferal species	Environment	Water depth (metres)
EOCENE	3	227 - 222	Bulimina brevispina Gaudryina hiltermanni Korobkovella grosserugosa Orisodorsalis ecuadorensis Osangularia pteromphalia Vaginulina decorata	Upper Slope ↑ Outer Shelf	600 ↑ 200
LATE PALAEOCENE	8 - 4	304 - 270	Cibicidoides alleni Cibicidoides succedens Gavelinella danica Gyroidinoides subangulata Osangularia expansa	Outer Shelf ↑ Middle Shelf	200 ↑ 30
	9	311 - 304	Alabamina midwayensis Cibicides simplex Operculina sp. Pararotalia tuberculifera	↑ Inner Shelf	↑ <30

Figure 12.6 Subsidence history of Rockall Plateau in the early Palaeogene revealed by the succession of foraminiferal assemblages in JOIDES borehole 117. After Berggren (1974b)

interpretation of the Thanet cycle. In particular, the combination of alpha index with wall structure percent and species number proves to be a valuable tool in distinguishing between low salinity regions and normal marine environments with restricted bottom conditions. Their use is also a corrective to interpretations based on 'indicator' genera alone, i.e. the presence of *Gyroidinoides, Pullenia* and *Alabamina* which could lead to suggestions of deep-water, even slope conditions. This is particularly important when biofacies interpretations in the Tertiary of the North Sea Basin are considered.

It seems unlikely that temperature was a restricting factor, despite the northern embouchure of the basin, although this was considered by Haynes (1958c) following Chavan (1946) and by Murray and Wright (1974). Oxygen isotope work (see chapter 14) suggests that world climates had recovered from the dramatic temperature fall at the Mesozoic/Tertiary boundary by the late Palaeocene and reached optimum towards the Middle Eocene. The forests clothing the surrounding delta plains were clearly subtropical to tropical (Reid and Chandler, 1933; Montford, 1970), although perhaps of a special high latitude type (Daley, 1972). The warmth of the Northern Atlantic is indicated by the occurrence of larger Foraminifera such as *Asterocyclina* north to latitude 54° in the N.E. Atlantic during the Middle to Upper Eocene (Dobson *et al.*, 1976), in agreement with the oxygen isotope results for the Cuisian of the Paris Basin (25°C) by Tivollier and Letolle (1968).

An interesting comparison can be made between these results for formations deposited in the shallow, semi-enclosed Anglo-French – Belgian Basin and those obtained by Berggren (1974b) by analysis of the late Palaeocene and early Eocene sediments obtained from Rockall Bank in the N. Atlantic under the JOIDES programme of deep-sea drilling. As shown by figure 12.6, the characteristic species, again mainly small rotaliids, reveal the history of early subsidence from 0 to 200 m. Deepening continued to reach bathyal depths by the Oligocene (Berggren and Aubert, 1976). This underlines the claim made by Douglas (1973) that benthonic Foraminifera, especially small rotaliids, because of their test construction and preservation characteristics, are the main source of information on the benthonic biostratigraphy of ancient deep-sea deposits. Moreover, they are more resistant to dissolution than the planktonic Foraminifera. 'For these reasons, they offer an excellent basis for biostratigraphic correlation, especially to supplement planktonic biostratigaphy.'

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SUMMARY CLASSIFICATION

MAIN FAMILIES AND IMPORTANT GENERA OF ROTALIIDS (SMALL)

ROTALIIDA	wall calcitic, hyaline perforate, radial, oblique or compound, bilamellar and may develop septal flap and canal system; planispiral or trochospiral to spreading or arborescent, annular discoid or annular complex; aperture characteristically ventral umbilical or basal and may extend over periphery on to dorsal side, multiple in advanced forms; Trias. – Rec. Key figures 12.7 – 12.9.
SPIRILLINACEA	planispiral to conical, undivided tube, biserial in adult or septate throughout with 2 or 3 chambers in each whorl; wall optically a single crystal; Trias. – Rec. Key figure 12.7.
SPIRILLINIDAE	unilocular (proloculus and undivided tube); aperture at open end of tube; Trias. – Rec.
Spirillina (no. 1)	planispiral, evolute; Trias. – Rec. (trochoid = *Turrispirillina;* with ventral umbilicus filled with laminated calcite also = *Alanwoodia,* Rec.).
PATELLINIDAE *nom. transl.* Copestake in Copestake and Johnson 1981	undivided tube followed by biserial arrangement or septate throughout with 2 chambers in each whorl; Cret. – Rec.
Patellina (nos. 2/3)	conical with 2 long, low chambers in each whorl in adult with incomplete chamberlets; ventral side involute, aperture umbilical beneath markedly hooked lobe; Jur. – Rec. (without incipient chamberlets = *Patellinoides,* Rec.).
DISCORBACEA	trochospiral, ventral side involute, dorsal side evolute; aperture ventral umbilical to extra-umbilical, there may be supplementary peripheral apertures; Cret. – Rec. Key figure 12.7.
DISCORBIDAE	aperture opens beneath umbilical lobe with distal arch and proximal notch; umbilicus open or closed by fusion of umbilical lobes or by boss; ventral side usually flattened or concave; Cret. – Rec.
Rosalina (nos. 4 – 6, 9/10)	umbilicus open; Cret. – Rec. (umbilicus with boss = sub. gen. *Gavelinopsis;* adult with inflated chamber = *Tretomphalus,* Rec., adult chambers long and low, 3 only in each whorl = *Neoconorbina,* Pal. – Rec.; suppl. peripheral aperture = *Discorbitura,* Olig.; partially involute on dorsal side, slightly evolute on ventral = *Discorbinella* (no. 11), Rec.).
Discorbis (nos. 7/8)	umbilicus closed by fusion of umbilical lobes or mass of secondary calcite; Eoc. – Rec.
CANCRISIDAE *nom. transl.* (Cancrisinae Chapman, Parr and Collins 1934)	biconvex, ventral side raised; aperture umbilical/extra-umbilical largely covered by lobe of final chamber or subtriangular flaps from chambers of last whorl; Cret. – Rec.

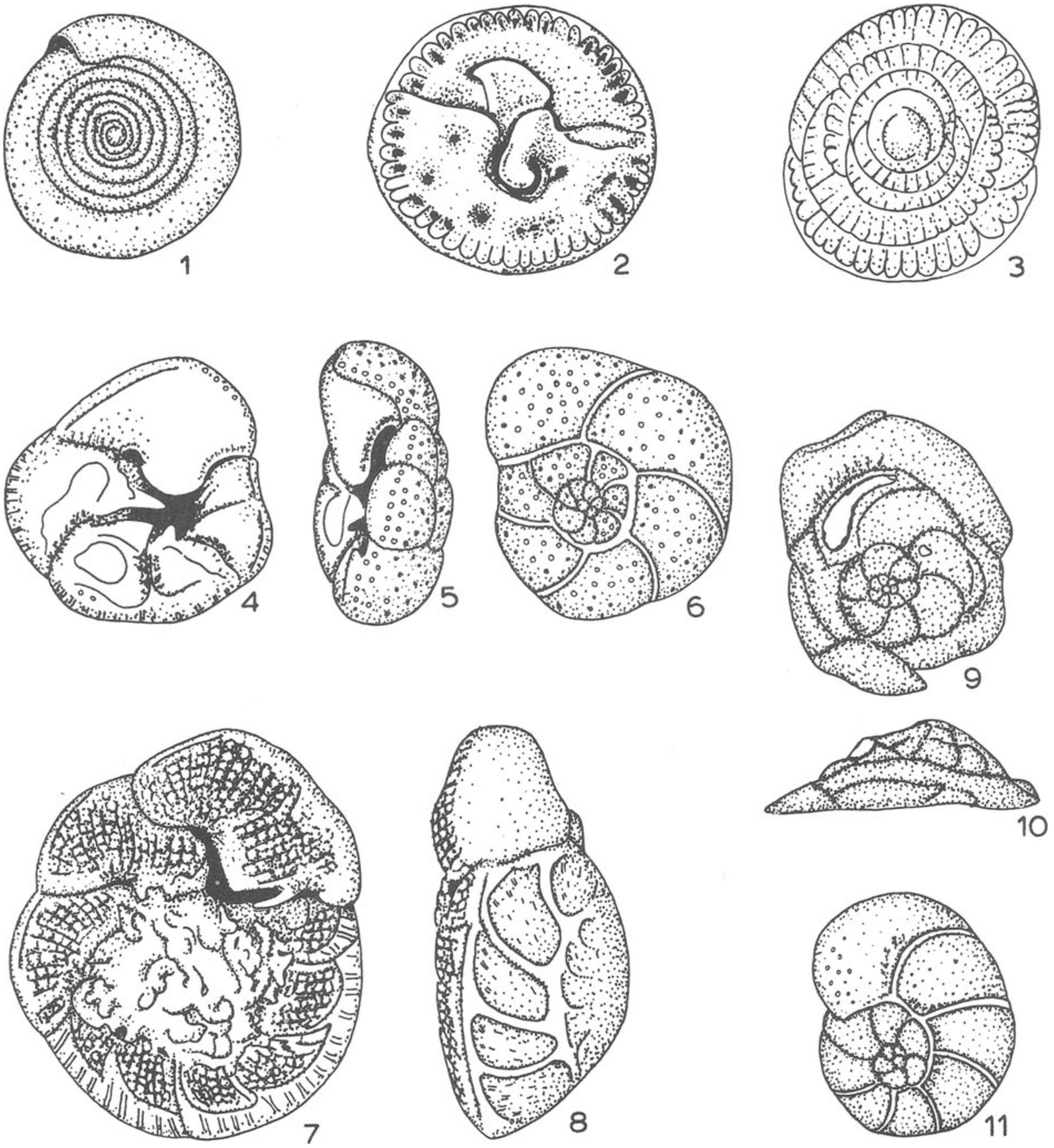
Cancris (nos. 14 – 16)	aperture beneath single lobe from last chamber; adult chambers high, periphery angular or keeled; poreless patch extending from lobe into apertural face; Eoc. – Rec.
Valvulineria (nos. 12/13)	umbilicus covered by single lobe of last chamber; rounded periphery, chambers only slowly increasing in size as added; Cret. – Rec.
Gyroidina (no. 17)	two apertures, 1 umbilical beneath triangular chamber lobe, 1 at basal suture midway between umbilicus and periphery with lip; Cret. – Rec. (single umbilical to extra-umbilical aperture extending to the periphery = *Gyroidinoides;* aperture extending just over periphery and sutures limbate = *Gavelinella,* Cret. – Mio.).
BAGGINIDAE *nom. transl.* (Bagginінae Cushman 1927)	aperture umbilical, simple; commonly with radiating striae in umbilical area and ornamented dorsal side; Cret. – Rec.
Baggina (nos. 18/19)	biconvex, rounded periphery; poreless area above simple aperture; Cret. – Rec.
Glabratella (nos. 20 – 22)	radiating striae in umbilical area; biconvex, rounded periphery; Eoc. – Rec. (high spire = *Angulodiscorbis,* Rec.; carinate with limbate sutures = *Heronallenia,* Rec.).
CYMBALOPORIDAE	conical, adult annular with alternating chamberlets or completely annular chambers with partitions; apertures multiple, umbilical, beneath coverplate or along ventral sutures; U. Cret. – Rec.
Cymbalopora (no. 23)	low conical, apertures umbilical; U. Cret. – Rec. (high conical, umbilicus covered with stellate plate and apertures sutural = *Cymbaloporetta* (nos. 24 – 26), Mio. – Rec.; umbilicus filled with horizontal lamellae = *Halkyardia,* Eoc; chambers cyclical with horizontal and vertical partitions = *Fabiania,* Eoc.).
ASTERIGERINACEA n. superfam.	trochospiral to planispiral and uncoiled; umbilicus closed; aperture ventral basal, simple or with extension(s) into the apertural face, or areal; supplementary chambers may occur on ventral side; Cret. – Rec. Key figures 12.7 and 12.8.
EPONIDIDAE	aperture simple, ventral basal or areal; Cret. – Rec.
Eponides = *Conorbina* (nos. 27 – 29)	trochospiral, biconvex, angular or keeled, may develop pseudumbilicus; aperture ventral basal; Cret. – Rec. (later chambers uniserial and aperture terminal = *Rectoeponides,* Eoc. – Rec.; aperture cribrate = *Poroeponides,* Plio. – Rec.; high, conical, ventral side also = *Cribrogloborotalia,* Eoc.; supplementary sutural apertures = *Oridorsalis,* Eoc. – Rec.).
ALABAMINIDAE	aperture ventral basal with extensions into apertural face or with folds; Cret. – Rec. Key figure 12.8.
Alabamina (nos. 1/2)	aperture a ventral basal slit with deep fold near periphery in median line; Cret. – Rec. (conical with fold near pseudumbilicus = *Globorotalites,* Cret.; coarsely perforate also = *Conorotalites*).

Charltonina (nos. 3/4)	aperture ventral basal and curving up into apertural face beneath lip; U. Cret. – Pal. (apertural extension strongly continued in median line = *Osangularia,* Cret. – Rec.).
SIPHONINIDAE	trochospiral to uncoiled uniserial or biserial; aperture ventral marginal in median line to offset terminal; U. Cret. – Rec.
Siphonina (plate 2B, no. 28)	trochospiral with fimbriate keel; aperture ventral near the periphery and produced with phialine lip; Palaeocene – Rec. (aperture without neck = *Pulsiphonina,* U. Cret. – Rec.; adult uncoiled uniserial with subterminal aperture = *Siphoninella,* M. Eoc. – Rec.; adult uncoiled biserial = *Siphonides* (no. 20), M. Eoc.).
ASTERIGERINIDAE	internal toothplates cut off supplementary chamberlets in umbilical area, one to each primary chamber; aperture ventral basal; Cret. – Rec.
Asterigerinata (nos. 5 – 7)	small supplementary chamberlets; usually biconvex or with raised dorsal side; Cret. – Rec. (large supplementary chamberlets and high umbonate, ventral side = *Asterigerina,* Eoc. – Rec.; very low trochoid and involute (asymmetrically lenticular) with numerous chambers and lobed sutures = *Amphistegina,* Eoc. – Rec.).
ORBITOIDACEA	umbilicus closed; most genera attached by dorsal side which becomes flat; aperture basal ventro-median to medio-dorsal, with supplementary marginal or peripheral openings or multiple; trochospiral to almost planispiral, annular discoid or complex in advanced forms or encrusting to arborescent; wall commonly compound; Cret. – Rec. Key figures 12.8 and 12.9.
ANOMALINIDAE	low trochospiral to almost planispiral or uncoiled uniserial or irregular, aperture basal ventro-median to medio-dorsal, may have additional marginal or peripheral openings; Cret. – Rec. Key figure 12.8.
Anomalinoides (nos. 11 – 13)	very low trochospiral, biconvex with rounded periphery, partially involute on dorsal side with boss; aperture ventral to dorsal, extending along spiral suture beneath lappets; U. Cret. – Rec.; additional peripheral aperture also = *Anomalinella,* Mio. – Rec.).
Cibicides (nos. 8 – 10)	low trochoid with flat, evolute 'dorsal' side; aperture medio-dorsal; Cret. – Rec. (biconvex = *Cibicidoides;* dorsal side partially involute = *Cibicidina;* adult uncoiled uniserial with multiple apertures = *Rectocibicides* (no. 18), Mio.; adult irregularly biserial with subterminal aperture = *Dyocibicides* (no. 19), Eoc. – Rec.; prominent dorsal lappets = *Hanzawaia,* Mio. – Rec.; compressed with keel and partially evolute on both sides = *Planulina,* aperture extending beneath lappets along spiral sutures on both sides also = *Hyalinea*, Quat.).

Heterolepa (nos. 14/15)	low trochospiral, biconvex, dorsal side evolute; aperture ventro-median; Cret. – Rec. (dorsal side flat with raised sutures = *Stensioina,* U. Cret.).
Annulocibicides (nos. 16/17)	initial chambers like *Cibicides,* later chambers irregularly elongate, finally annular; apertures multiple, peripheral; Mio. (apertures on 'dorsal' attachment side = *Cyclocibicides,* Rec.; regular large openings only, no fine perforations = *Cycloloculina,* Pal. – Mio.).
PLANORBULINIDAE	low trochospiral to annular discoid with alternating chamberlets and multiple apertures; Eoc. – Rec. Key figure 12.8.
Planorbulina (nos. 21 – 23)	low trochospiral to annular discoid with alternating chamberlets; 'dorsal' attachment side flat, 'ventral' side raised; 2 peripheral apertures to each chamberlet at septal sutures; Eoc. – Rec. (biconvex with deposits of secondary calcite on 'ventral' side = *Planorbulinella*).
Linderina (no. 26)	annular discoid with alternating chamberlets forming central layer with thick lamellae on each side; Eoc. – Mio.
ACERVULINIDAE	low trochospiral or discoidal to encrusting with 1 or more layers of inflated or elongate chambers, forming irregular or rounded mass; apertures replaced by coarse perforations; Eoc. – Rec.
Acervulina (no. 24)	trochospiral to irregularly encrusting with inflated chambers; Neo. – Rec. (later chambers elongate and reniform = *Planogypsina;* layers of polygonal chambers forming hemispherical or rounded test = *Gypsina* (no. 25), Eoc. – Rec.).
HOMOTREMATIDAE	irregularly trochospiral to arborescent with flat 'dorsal' attachment surface; aperture basal, ventro-median or cribrate; U. Cret. – Rec. Key figure 12.9.
Rupertina (no. 1)	low trochoid to loosely spiral with irregular basal apertural slit; flat 'dorsal' attachment surface with marked flange; ?Eoc. – Rec. (adult uniserial with tubular apertures = *Biarritzina,* Eoc. – Rec.).
Carpenteria (nos. 2 – 5)	low conical to spreading with inflated irregular chambers; flat attachment surface with flange; aperture a low, ventral basal slit extending into a rounded umbilical opening; U. Cret. – Rec.
Homotrema (no. 6)	encrusting with coarse, truncated branches; chambers in roughly concentric layers with cribrate areolae, Rec. (slender with scattered pores of two sizes = *Miniacina*).
NONIONACEA Loeblich and Tappan 1974	umbilicus open or closed, when open usually secondarily closed by single chamber lobe, coverplate of fused umbilical lobes, boss or granules but may then be canaliculate; trochospiral to involute planispiral; aperture basal, ventral to median; advanced forms with supplementary apertures, retral processes, septal pits, bars and canals; Cret. – Rec. Key figure 12.9.

CHILOSTOMELLIDAE	umbilicus closed; trochospiral to involute planispiral with few chambers in each whorl; aperture basal ventral to median, with lip; Cret. – Rec.
Allomorphina (nos. 7/8)	low trochospiral, involute, 3 chambers per whorl; aperture a low slit; Cret. – Rec. (planispiral with median aperture = *Allomorphinella,* U. Cret.).
Pullenia (nos. 20/21)	planispiral with aperture a low slit extending to umbilicus on each side; U. Cret. – Rec.
Chilostomella (nos. 9/10)	trochospiral to biserial with chambers becoming inflated and embracing; aperture a ventral basal slit; U. Cret. – Rec. (aperture round = *Chilostomelloides,* Palaeocene – Mio).
NONIONIDAE	trochospiral to planispiral, umbilicus open or secondarily closed with final chamber lobe, granules or boss; aperture basal, ventral to median; Cret. – Rec.
Nonionella (nos. 13/14)	low trochoid, auriculate with rounded periphery; chambers rapidly increasing in height, last one extending into umbilicus (may be fistulose); aperture a low, ventral basal slit; Cret. – Rec. (final chambers planispiral = sub. gen. *Nonionellina* (nos. 15/16), Mio – Rec.).
Nonion (nos. 11/12)	planispiral with rounded to subangular periphery, umbilicus granulate or embossed; aperture median; Cen. (open umbilicus also = *Melonis*).
ELPHIDIIDAE	Planispiral to trochospiral and uncoiled, umbilicus secondarily closed by granules, fused lobes forming coverplate or canaliculate boss; advanced forms with retral processes, sutural pits, septal flap and canals and supplementary umbilical apertures; aperture a basal median arch or multiple; Palaeocene – Rec. Key figure 12.9.
Protelphidium (figure 12.1)	planispiral; umbilicus filled by fused umbilical flaps and granules forming coverplate with intercommunicating umbilical cavities; aperture a basal median slit; wall radial; Palaeogene (granules absent = *Astrononion*, Eoc. – Rec.).
Haynesina Banner and Culver 1978 (nos. 18/19 and plate 2B, no. 22)	planispiral, umbilicus narrow, granulate; sutural fissures deep and partially bridged by extensions of the wall of subsequent chambers, forming 'intercameral lacunae'; supplementary umbilical apertures open into lacunae; wall radial or oblique, primary aperture a basal, median slit; Neogene – Rec.
Elphidium (nos. 22 – 24 and plate 8, nos. 8 – 13)	planispiral, umbilicus with canaliculate boss; sutural fissures crossed by septal bridges (marking internal retral processes) giving septal canal communicating to exterior via septal pits, spiral canal and umbilical openings; septal flap partial; apertures multiple, basal median; Eoc. – Rec. (solid septal bars and without retral processes *Cribrononion,* Neo. – Rec.; aperture areal also = *Cribroelphidium,* Neo. – Rec.; anastomosing canals = *Parrellina,* Olig. – Rec.; adult uncoiled = *Ozawia,* Rec.).

Elphidiella (no. 17)	planispiral with double row of septal pits; retral processes absent; aperture multiple, areal; Palaeocene – Rec. (retral processes present and septal flap fully developed = *Cellanthus,* Plio. – Rec.; asymmetrically planispiral = *Laffiteina,* Palaeocene).
Faujasina (nos. 25 – 27)	trochoid with flat dorsal side and spiral canals on both sides; apertures multiple, ventral basal; Plio. (ventral umbilicus filled by septal flaps with tiny irregular septal pits which may occur in double row; ornament of anastomosing ribs = *Polystomellina* (= *Notorotalia*), Mid. Eoc. – Rec.).



Key figure 12.7 **Rotaliida (Smaller), Spirillinacea, Discorbacea, Asterigerinacea**

1 ***Spirillina vivipara*** **Ehrenberg, after L. & T., × 150**

2/3 ***Patellina corrugata*** **(Williamson), ventral and dorsal views, × 100**

4 – 6 ***Rosalina anomala*** **Terquem, ventral, peripheral and dorsal views, after Haynes, × 100**

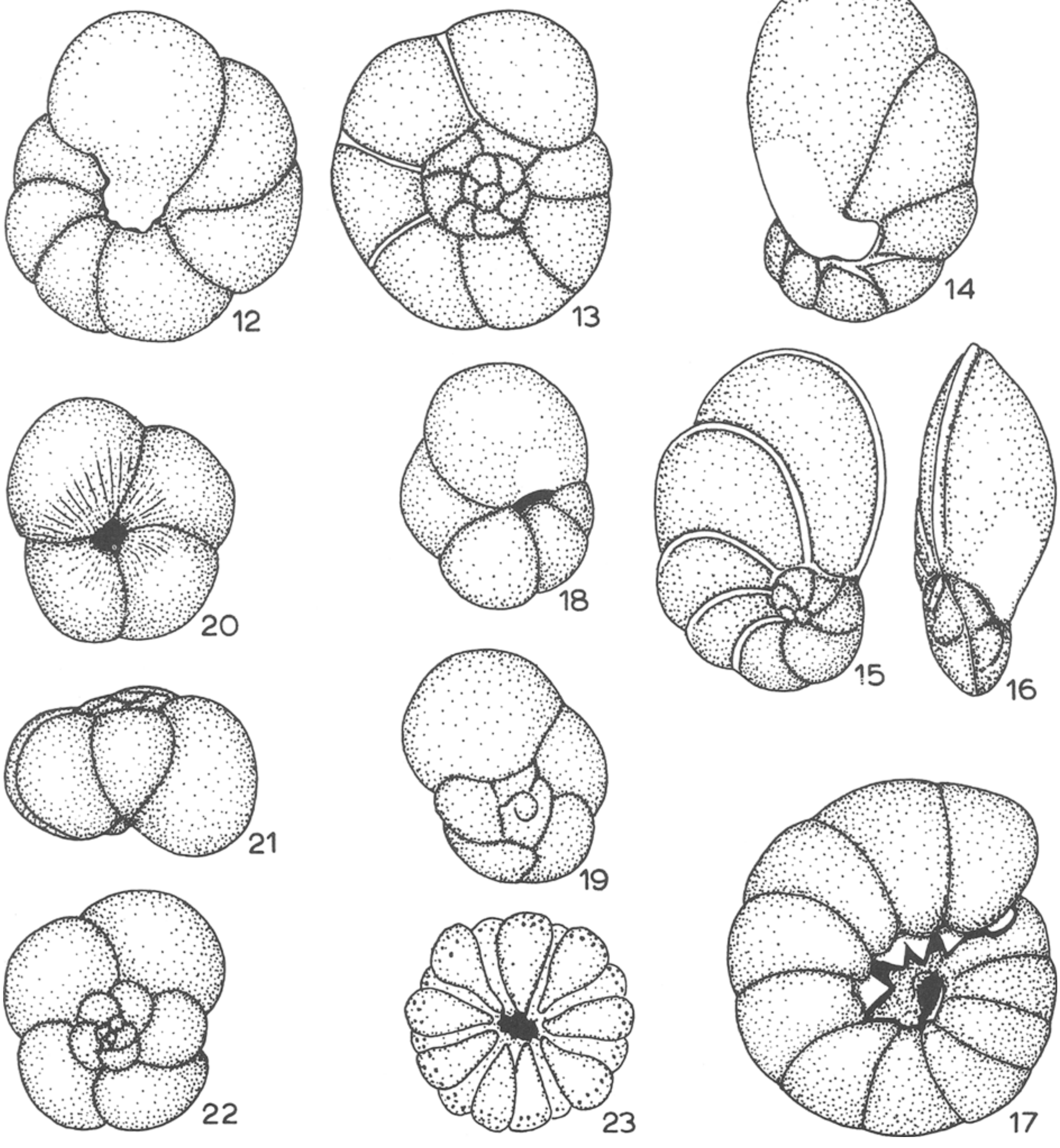
7/8 ***Discorbis wrightii*** **(Brady), ventral and peripheral views, after Haynes, × 160**

9/10 ***Rosalina globularis irregularis*** **(Rhumbler), dorsal and peripheral views, after Haynes, × 100**

11 ***Discorbinella*** **sp., dorsal view, after Haynes, × 100**

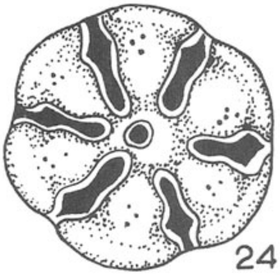
(continued overleaf)

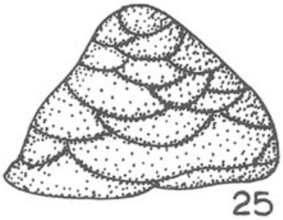
Key figure 12.7 ***(continued)***

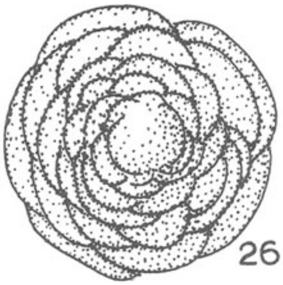


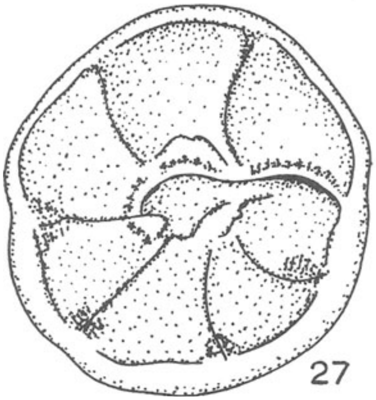
12/13 *Valvulineria californica* Cushman, ventral and dorsal views, after L. & T., × 130
14 – 16 *Cancris oblongus* (Williamson), ventral, dorsal and peripheral views, after Haynes, × 66
17 *Gyroidina orbicularis* d'Orbigny, ventral view, after L. & T., × 100
18/19 *Baggina californica* Cushman, ventral and dorsal views, after L. & T., × 56
20 – 22 *Glabratella crassa* Doreen, ventral, peripheral and dorsal views, after L. & T., × 120
23 *Cymbalopora bradyi* (Cushman), ventral view, after Brady, × 50

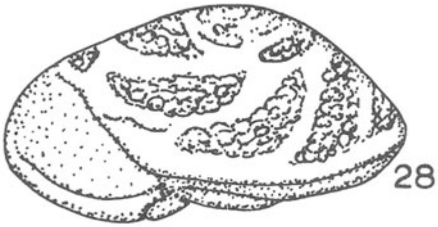
Key figure 12.7 ***(continued)***

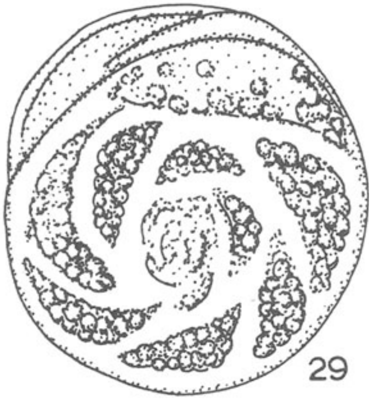






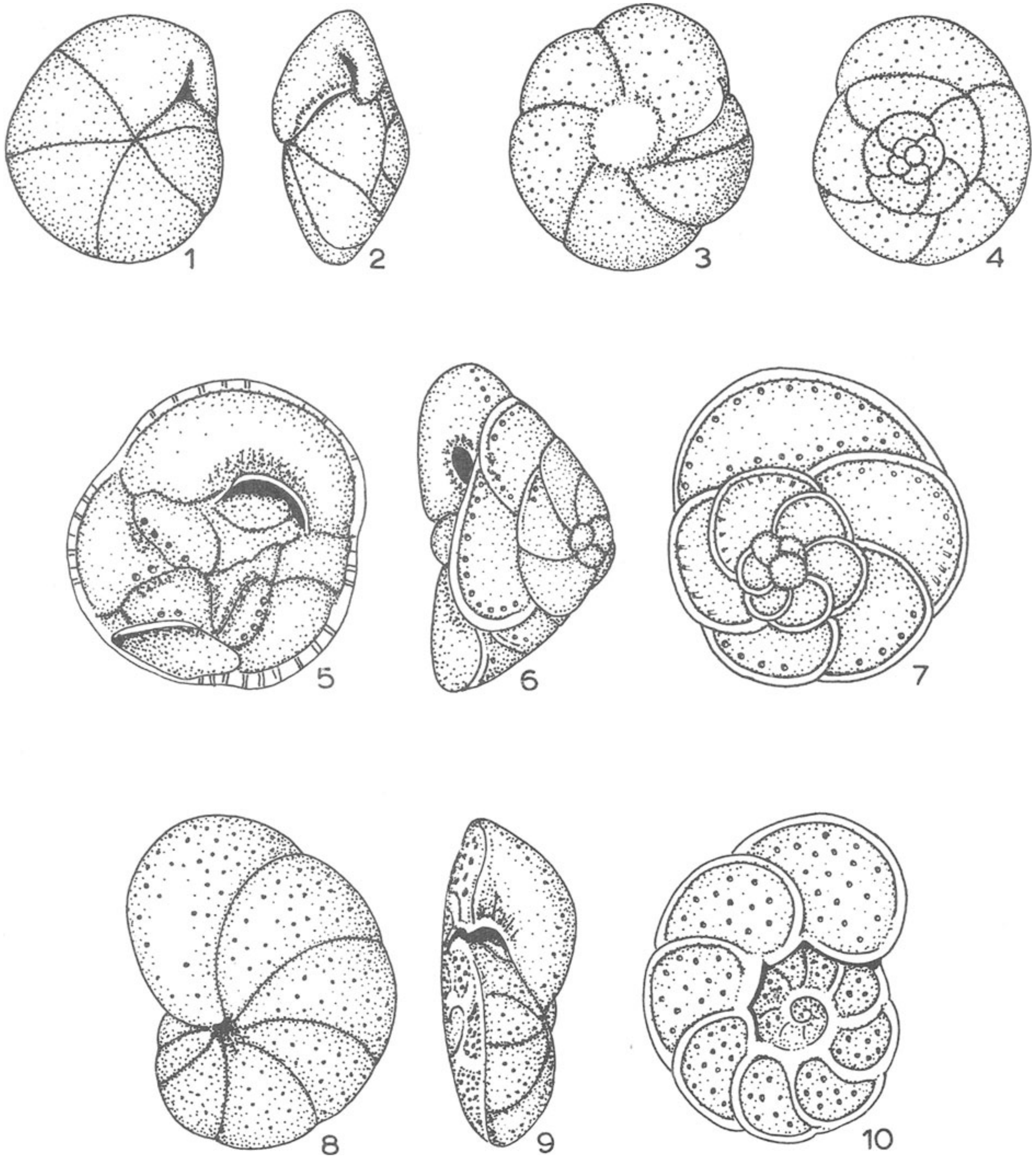






24 – 26 ***Cymbaloporetta squammosa*** **(d'Orbigny), ventral, peripheral and dorsal views, after Brady, × 50**

27 – 29 ***Eponides repandus concameratus*** **(Montagu), ventral, peripheral and dorsal views, after Haynes, × 40**



Key figure 12.8 **Rotaliida (Smaller), Asterigerinacea, Orbitoidacea**

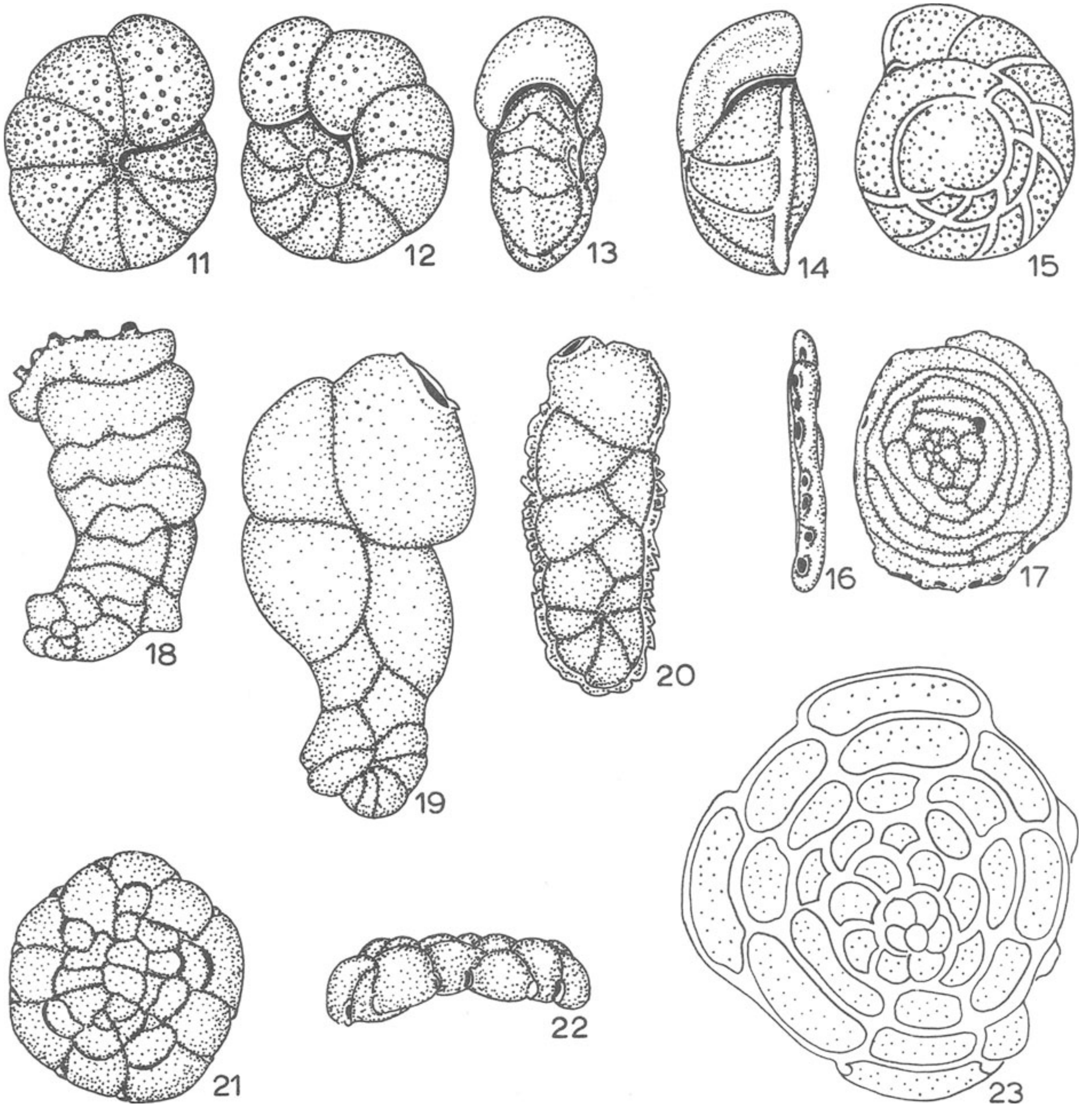
1/2 ***Alabamina obtusa*** **(Burrows & Holland), ventral and peripheral views, after Haynes, × 100**

3/4 ***Charltonina canterburyensis*** **Haynes, ventral and dorsal views, × 200**

5–7 ***Asterigerinata mamilla*** **(Williamson), ventral, peripheral and dorsal views, after Haynes, × 200**

8–10 ***Cibicides lobatulus*** **(Walker & Jacob), ventral, peripheral and dorsal views, after Haynes, × 160**

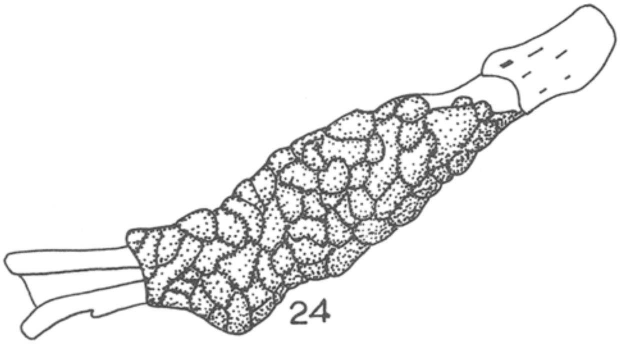
Key figure 12.8 *(continued)*



11 – 13 ***Anomalinoides pinguis*** **Jennings, ventral, dorsal and peripheral views, after L. & T., × 70**
14/15 ***Heterolepa dutemplei*** **(d'Orbigny), peripheral and dorsal views, after L. & T., × 37**
16/17 ***Annulocibicides projectus*** **Cushman & Ponton, peripheral and dorsal views, after L. & T., × 37**
18 ***Rectocibicides miocenicus*** **Cushman & Ponton, ventral view, × 50**
19 ***Dyocibicides biserialis*** **Cushman & Valentine, ventral view, after Brady, × 50**
20 ***Siphonides biserialis*** **Feray, ventral view, after L. & T., × 200**
21 – 23 ***Planorbulina distoma*** **Terquem, ventral, peripheral and dorsal views, after Haynes, × 65**

(continued overleaf)

Key figure 12.8 ***(continued)***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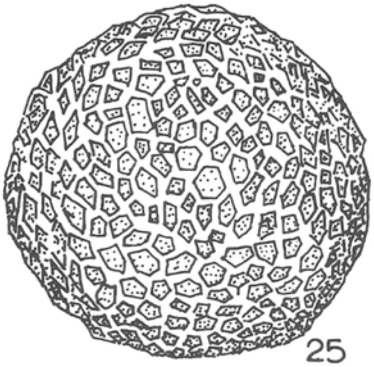
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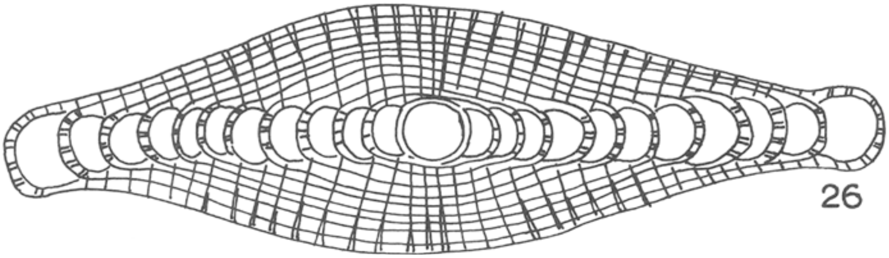
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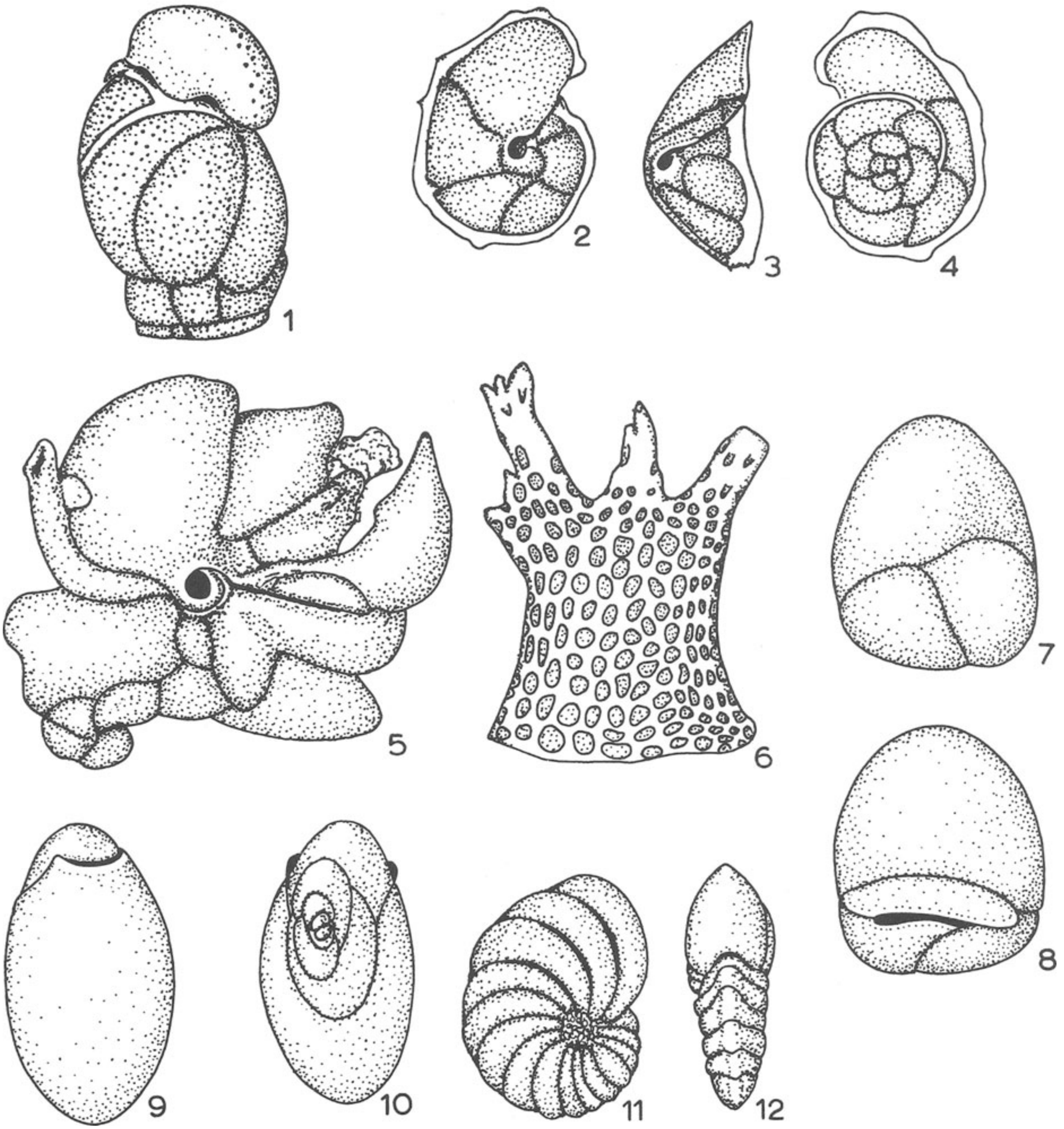
24 ***Acervulina inhaerens*** **Schultze, after Brady, × 30**
25 ***Gypsina vesicularis*** **(Parker & Jones), after Brady, × 30**
26 ***Linderina brugesi*** **Schlumberger, axial section, diagrammatic, × 150**



Key figure 12.9 **Rotaliida (Smaller), Orbitoidacea, Nonionacea**

1 ***Rupertina stabilis*** **(Wallich), side view, after L. & T., × 40**

2–4 ***Carpenteria balaniformis*** **Gray, ventral, peripheral and dorsal views, after L. & T., × 20**

5 ***Carpenteria monticularis*** **Carter, ventral view, after Brady, × 12**

6 ***Homotrema rubrum*** **(Lamarck); diagrammatic side view, × 20**

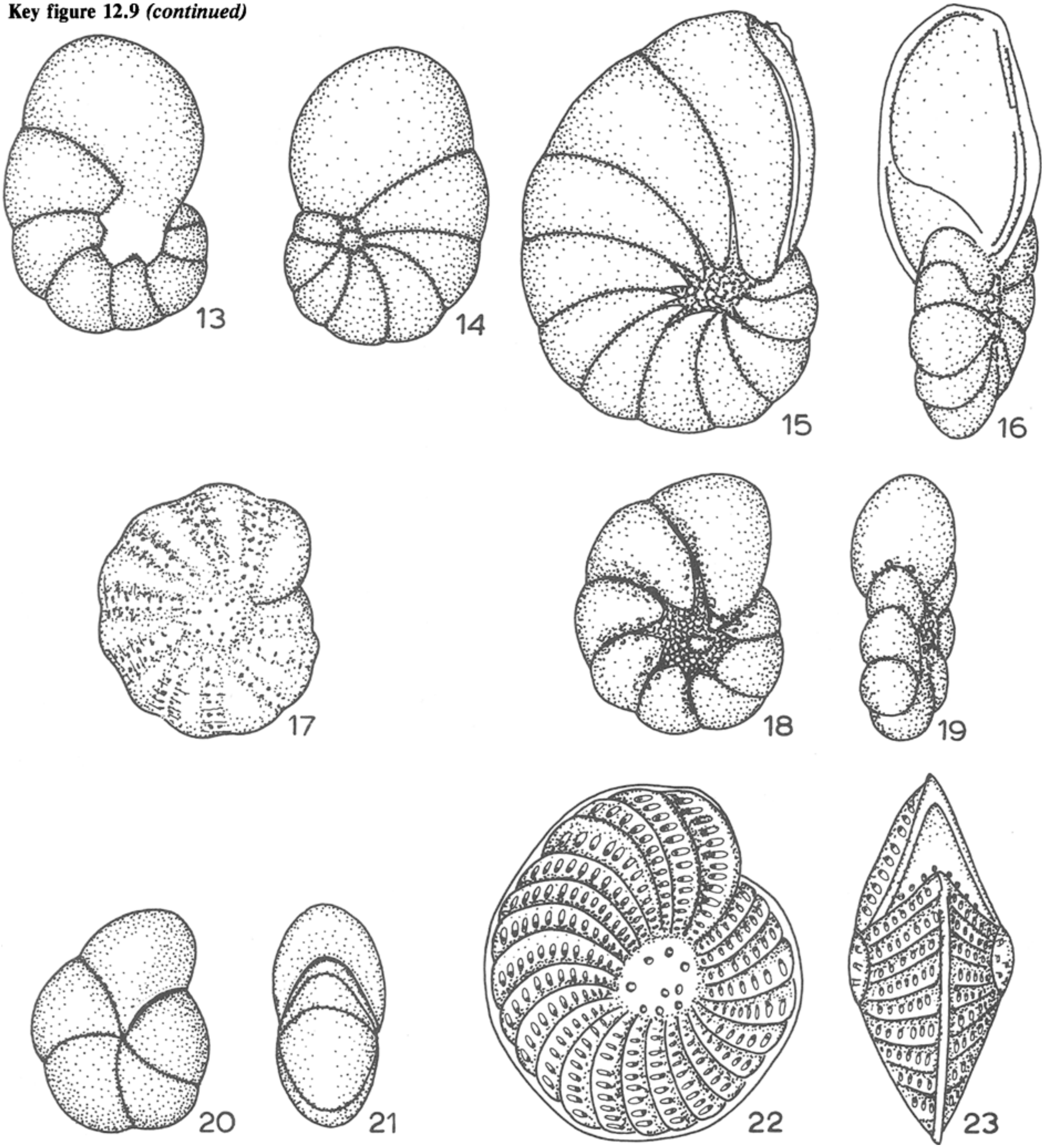
7/8 ***Allomorphina contraria*** **Reuss, dorsal and ventral views, after L. & T., × 78**

9/10 ***Chilostomella oolina*** **Schwager, ventral and dorsal views, after Brady, × 50**

11/12 ***Nonion boueanum d'Orbigny,*** **side and peripheral views, after Brady, × 70**

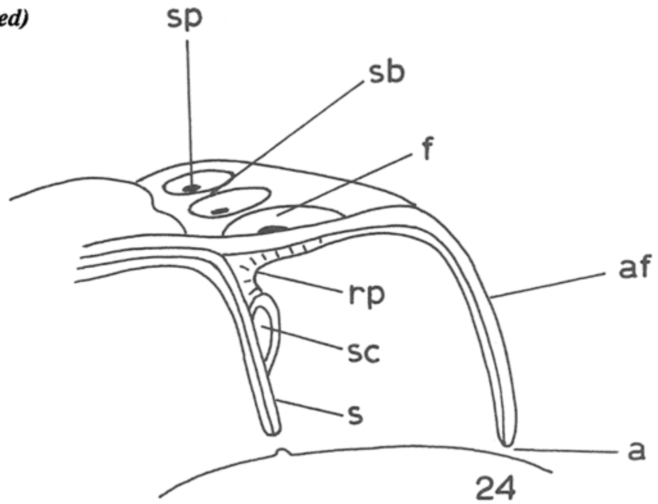
(continued overleaf)

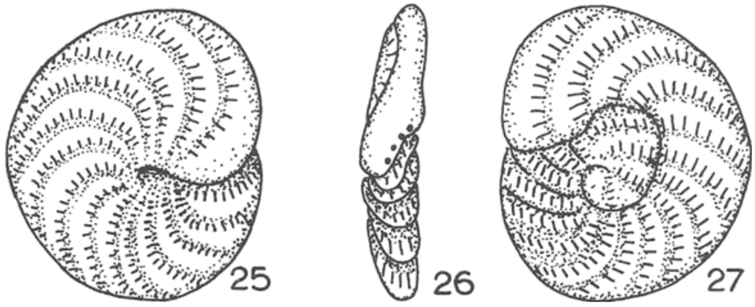
Key figure 12.9 ***(continued)***



13/14 *Nonionella turgida digitata* **Nørvang, ventral and dorsal views, after Haynes, × 150**
15/16 *Nonionellina* **sp., side and peripheral views, after Haynes, × 100**
17 *Elphidiella arctica* **(Parker & Jones), side view, after Brady, × 30**
18/19 *Haynesina depressula* **(Walker & Jacob), side and peripheral views, after Haynes, × 100**
20/21 *Pullenia quinqueloba* **(Reuss), side and peripheral views, after Haynes, × 66**
22/23 *Elphidium crispum* **(Linné), side and peripheral views, after Cushman, × 25 (approx.)**

Key figure 12.9 ***(continued)***





24 ***Elphidium,*** **diagram of cutaway chamber to show septal canal (sc), retral processes (rp), septal pits (sp) opening into depressions or fossettes (f) and separated by septal bar (sb). Septal canal formed by infolding of partial septal flap against septum (s). Apertural face (af), aperture (a)**

25 – 27 ***Faujasina carinata*** **d'Orbigny, ventral, peripheral and dorsal views, × 50**

Chapter 13

The Rotaliida (Larger)

> The taxonomically most valuable features are those which are, at any stage in the evolution of the group (orbitoids) combined, 'correlated', with the greatest number of other distinctive features and which enable us to recognize a sequence of distinctive forms occurring in stratigraphic order.
>
> (Glaessner, 1945)*

I arrived at 7.30 a.m., as usual, at the Esso/Libya Micropalaeontological Laboratories in Tripoli, the winter sun striking low through the black silhouettes of the date palms. But before I could start work on samples from our latest wildcat, Esso Zelten C1 – 6, which was still drilling ahead in Sirtica, I had a telephone call from the Exploration Manager. Would I go to the warehouse and collect some core just delivered from the rig by air and 'check out the age', as soon as possible. On arrival at the warehouse I opened up one of the 5 ft (1.5 m) wooden core boxes and picking up a short length of broken core immediately found that it contained nummulites of the large size characteristic of the Middle Eocene. On returning to the laboratories, a quick appraisal of the external characters of the test and of the whorls and chamber shapes in some naturally split sections confirmed they were the Middle Eocene species *N. gizehensis*. I was thus able to pass on the needed biostratigraphical information the same morning.

The nummulitic limestone of the core was stained brown with contained oil and the interval tested at 200 barrels a day. This was 'not commercial', so drilling went ahead because we knew by extrapolation from previous exploration drilling that a thick, Lower Tertiary section should be present below the Middle Eocene. Eventually, after penetrating more than 1500 ft (457 m) of nummulitic and alveoline limestone of Middle and Lower Eocene age, the drill penetrated on oil-saturated reefal limestone that tested at some 18 000 barrels a day (the sixth highest producer known at that time).

By good luck I was flown down to the rig while testing was being carried out, en route to join a field party mapping in the same area. I was thus able to visit the resident well-site geologist and examine the latest ditch cuttings. They proved to contain numerous large rotaliids, including unmistakable specimens of *Miscellanea miscella* together with *Ranikothalia sindensis,* indicative of the uppermost Palaeocene. It was therefore immediately possible to inform the Exploration Manager, who relayed the information to headquarters in New York, of the age of the rocks forming the reservoir for this spectacular discovery well.

Of course it must be emphasised that it is not normally possible to identify and date assemblages of large rotaliids without lengthy preposition, including sectioning, but these examples will give an idea of the great utility of this group of forams, especially in the Tertiary rocks laid down in the great Tethyan seaway (see figure 13.6).

As pointed out in chapter 1, because of their macroscopic size the large rotaliids, in particular *Nummulites,* have been known since ancient times and stylised drawings of *Orbitoides* were made by Faujas St. Fond in 1779. However, despite (perhaps because of) the discovery that forams were protozoans, in 1835, the large Foraminifera including soritids as well as orbitoids remained classed with bryozoans and corals until the middle of the eighteenth century. Then, Carpenter (1850) was able to show conclusively that the orbitoids and nummulites were related and more likely to have been forams than bryozoans. He was also able to demonstrate, as discussed earlier, that they differed from the soritids in being perforate. However, *Omphalocyclus* remained under *Orbitolites* until Douvillé discovered that it was perforate in 1902. The lepidocyclines were first distinguished from *Orbitoides* by Ehrenberg (1856) but not as a separate family until 1932, by

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*See reprint (1963a).

Scheffen, although the genera (subgenera) were recognised earlier (Douvillé, 1911, 1915, 1924; Vaughan, 1924).

The stratigraphical value of the nummulites was recognised in the mid-nineteenth century, and studies were made of collections from Southern France and Switzerland (Harpe, 1879 – 83), Egypt and Libya (Harpe, 1883) and India (d'Archiac and Haime, the classic work of 1853 – 54). Notable early twentieth century studies include those made in Italy (Prever, 1902), Western Europe (Douvillé, 1906b), France and the Alps (Boussac, 1911a, 1911b) and Hungary (Rozlozsnick, 1929).

The application and study of the orbitoids came somewhat later and date from the turn of the century. Classic studies in America include Douvillé (1898), Vaughan (1924, 1929, 1933) and Vaughan and Cole (1932), and in the Far East, Newton and Holland (1899), Rutten (1911 – 14), Vlerk (1922) and Vlerk and Umbgrove (1927). Modern work is discussed below but particular note can be made here of the outstanding contribution of the 'Dutch School' to our understanding of the evolution and phylogeny of the orbitoids.

CHAMBER FORM AND COILING MODES

Large rotaliids exploit to a remarkable degree the architectural possibilities inherent in the hyaline, calcareous lamellar test and through mutual aid with symbiotic algae achieve some of the largest sizes known in the Foraminifera, up to 15 cm diameter in *Cycloclypeus*. The appearance of the septal flap (by infolding of the wall, as in the Nonionacea) to give the characteristic 'double septum' of this group leads to the formation of open canals = 'septal fissures' or subsutural, septal canals. Umbilical canals may be formed in the spiral gap between the whorls and umbilical plugs and spiral canals within the successive sheets of the spiral lamellae on either side of the test and at the periphery, these being represented by grooves on the original, primary lamella. The spiral canals are connected by radial canals formed by resorption through the lamellae (plate 12, nos. 5 and 6). As pointed out by Billman *et al.* (1978), these systems of canals allow direct communication between the early chambers and the exterior. This is manifestly important in symbiotic forms as it allows the later chambers to be bypassed and allows a division of function between different chambers and layers. Hottinger (1977a, 1978) has observed that genera with canal systems in contrast to those without, such as the large soritids, can remain mobile even when cytoplasm is withdrawn from the last chambers because connection can still be maintained with the external protoplasm and pseudopods.

As noted in chapter 4, the structural problems associated with large size are solved in different ways:

(1) By opening up of the umbilical area and its infilling by pillars, together with intercalation of extra whorls of small chambers in the spire.

(2) By chambers becoming subannular or annular rings subdivided into small chamberlets or replaced by rings (intersecting spirals) of small secondary chambers.

(3) By raising and vacuolisation of the spiral lamellae that tend to be built up in a thick mass on each side of the test and strengthening by cross-beams (pillars).

(4) As an alternative to (3), by suspension of the lamellae from a thickened marginal cord which allows light construction with thin spiral sheets on the sides.

By these architectural innovations the problems which would arise with the acquisition of very large chambers are avoided. While the volume of the test greatly increases, the volume of the chambers or chamberlets increases much more slowly and may even remain constant, although there is no overall correlation between number and volume (Hottinger, 1978). With increase in size Hottinger notes that 'the foraminifer must devise methods to shorten distances between the first and last components of its shell'. This is achieved by the development of a system of stolons (tubular foramina) which tend to possess bilateral or radial symmetry. In advanced forms a complicated crossover network is produced which presumably provides a means of separating cytoplasmic flowlines and facilitates transport in and out of the chambers.

The main coiling modes that result are conical, conical with intercalated whorls, annular conical, planispiral, subannular to annular discoid and complex and globular with lateral chamberlets only. The superfamilies and families are recognised on this basis together with the character of the canal system. (See the Summary Classification at the end of the chapter.) Note that certain families which show parallel development of annular complex structure but are apparently without septal flap and canal system (and of independent origin) are also included here.

Rotaliacea

This superfamily includes trochospiral to planispiral forms characteristically with marked septal fissures (which may extend into the test wall so that the whole surface becomes finely incised) or dense radial canals. Trochospiral to conical genera with the umbilical area filled with pillars are included in the Rotaliidae, involute planispiral forms, some with dense radial canals rather than fissures, in the Miscellaniidae. Globular trochospiral to planispiral genera with spines in the plane of coiling and thick lamellae or tiers of lateral chamberlets are included in the Calcarinidae. Annular conical arrangement is achieved in the Chapmaninidae, subannular complex arrangement in the fan-shaped Miogypsinidae and annular complex arrangement in the Lepidorbitoididae (see further below under orbitoidal structure).

Nummulitacea

This superfamily includes planispiral forms with marginal cord and well-developed spiral and subsutural septal canals and advanced forms with subannular to annular discoid or complex structure. The simple planispiral forms (with incipient development of chamberlets only) are included in the Nummulitidae. Here the marginal cord may be massively developed which allows drastic thinning of the side walls, usually combined with pronounced lateral compression. The spiral canals are confined to the marginal cord (marginal or peripheral canal system). In *Sulcoperculina,* the marginal cord is sulcate and produced into two plates that project into the chamber cavity.

Genera which are subannular discoid to complex or annular discoid with rectangular to hexagonal chamberlets are included in the Cycloclypeidae. Annular complex genera with rectangular to hexagonal chamberlets are included in the Discocyclinidae, and annular complex forms with radial rods in the equatorial layer in the Pseudorbitoididae. The marginal cord is largely lost in the annular genera, its support no longer being needed.

Two other major families with annular complex structure are the Orbitoididae and the Lepidocyclinidae. The genera in these families are without canal systems and have small arcuate to hexagonal chambers in the equatorial layer rather than annuli and chamberlets, so are considered to be unrelated to either the Rotaliacea or the Nummulitacea. However, modern opinion inclines to the view that both families arose from among the small rotaliids and the Orbitoididae are placed here with the Planorbulinidae (Orbitoidacea of the 'Treatise') and the Lepidocyclinidae with the Asterigerinidae (Asterigerinacea herein).

It is appropriate at this point to discuss in more detail the morphological features considered important in the Nummulitidae, in which the development of the marginal cord is a remarkable feature, and also the structure of the 'orbitoids' in which foraminiferal test architecture reaches its apogee. A proper study can only be made on the basis of thin sections and in most cases both vertical and equatorial (median) sections are required. Great care must be taken in interpretation of random sections and usually these will be found inadequate for identification and may, indeed, be misleading. Detailed examination of the canal system requires the making of internal casts (Carpenter, 1856). Great strides have been made recently in the interpretation of fine structures with the application of the SEM—see Bignot *et al.* (1972) and Hottinger (1977a, 1978).

Some of the features considered important in *Nummulites* and also in allied genera are shown in figure 13.1. In the *Nummulites* group the test is involute and, as in other planispiral involute genera, the chamber cavity (lumen) extends over previous whorls, referred to as the 'alar prolongation'. In *Assilina* which is evolute, the alar prolongation is pinched off although the lamellae may continue over previous whorls. Both are tightly coiled with low spires. Involute forms with loose (lax) coil and high spire, the diameter (*d* value of Davies, 1945) tending to double or more with each whorl, are referred to *Operculinoides,* evolute forms with loose coil and high spire to *Operculina.*

Authors have found difficulty in deciding on the generic limits in this family because of the problem of iterative evolution and parallel development along many lines (see, for instance, Caudri, 1944; Cizancourt, 1948; Cole, 1953, 1958, 1959, 1960, 1961; Nagappa, 1959; Smout and Eames, 1960). This led Cole to take an extreme position in the 'Treatise' and most of the genera previously recognised are lumped with *Nummulites,* including *Assilina, Operculina, Operculinella, Operculinoides* and *Ranikothalia* which are recognised as separate here. More recently, Hottinger (1977a) has attempted to base generic determination upon the stolon and canal system and goes so far as to claim that the

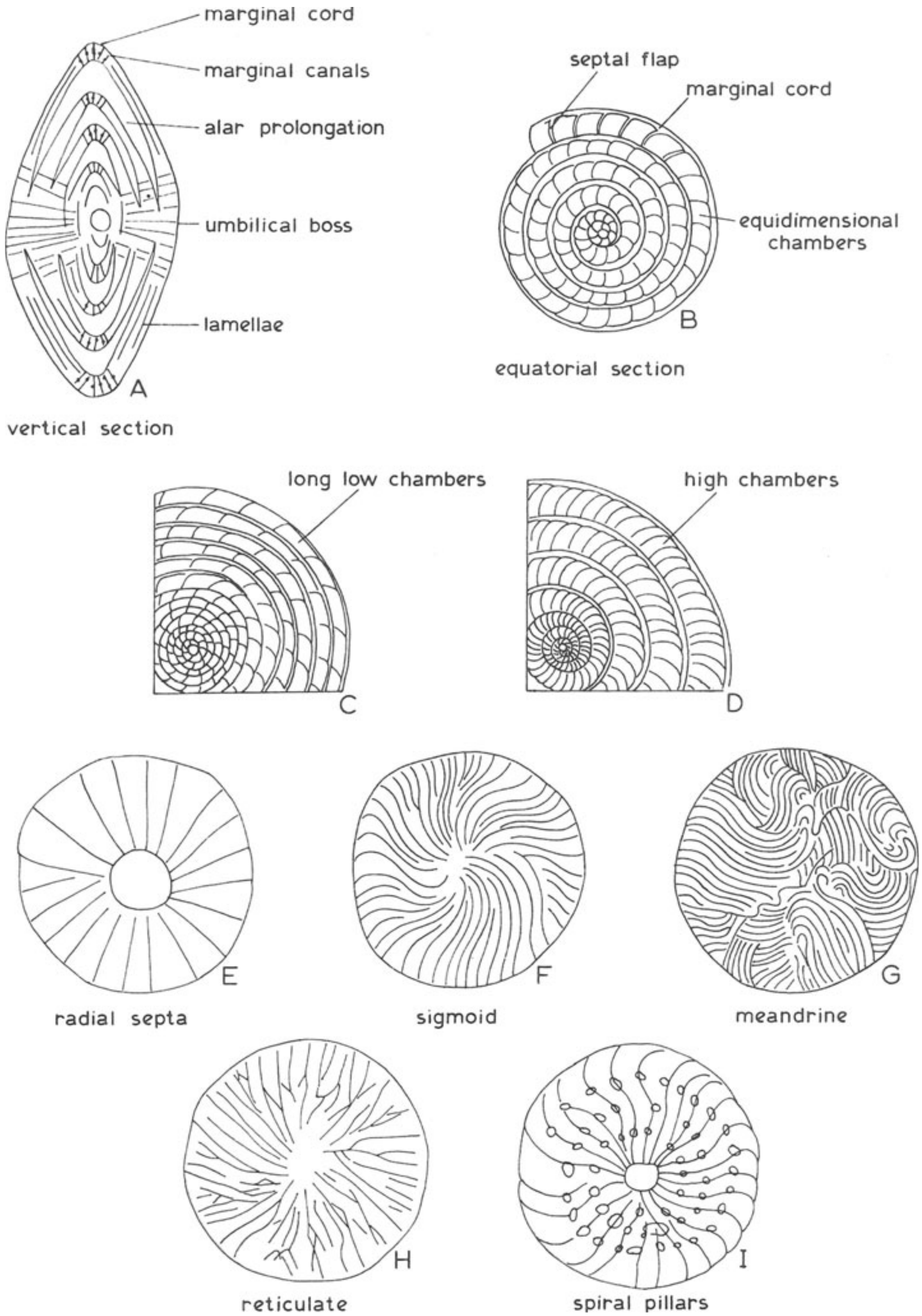


Figure 13.1 Basic morphology of the *Nummulites* group
A Vertical section based on *N. globulus*
B Equatorial section based on *N. praelaevigatus*
C Equatorial section (quadrant) based on *N. intermedius*
D Equatorial section based on *N. planulatus*
E – H Septal filaments in *N. deserti, N. laevigatus, N. gizehensis* and *N. intermedius*
I Pillars developed at junction of septal filaments and spiral cord in *N. partschi*
Note that most nummulitids are pillared to some degree

traditional definitions emphasising the involute or evolute nature of the coiling and presence or absence of secondary septa, should be abandoned. The cycloclypeids are therefore combined with the nummulitids and eight genera are recognised. This leads to the revival of *Ranikothalia*—coarse canal system and simple, vertical, sutural canals branching from subsutural (interseptal) canals, and *Operculina*—sutural canals forked or ramified, together with *Nummulites*—sutural canals ramified and causing imperforate traces on side walls (trabeculae), and a new genus *Planoperculina*—proximal sutural canals forked or ramified, distal sutural canals ramified and directed forwards. However, these features are clearly progressive and it is not manifest that they should take precedence over the traditional definitions. In the case of the cycloclypeids the new genus, *Heterocyclina* is distinguished from *Heterostegina* because it has L-shaped rather than Y-shaped stolons. But Y-shaped stolons also occur in *Spiroclypeus* and some *Cycloclypeus* species. Only advanced *Cycloclypeus* has diagonal, crossed over stolons (figure 13.2J). Again, this feature is clearly progressive and subject to variation at specific level. In practice, gross morphology has to be taken into account. It therefore seems best to attempt to combine traditional criteria with evidence of fine structure in a holistic approach, accepting that genera may grade into one another (as discussed in the case of the Nodosariidae, and in chapter 5 this is quite consistent with modern evolutionary theory). An additional advantage is the avoidance of wholesale reallocation of species to different genera.

Even when interpreted in the strict sense, *Nummulites* is a supergenus comprising some hundreds of species and subspecies. The relationships of these species are imperfectly known and although subgeneric or even generic distinctions would appear appropriate and were attempted by d'Archiac and Haime (1853) and Prever (1902), a sound basis for them is yet to be found. This is not only because of the problems of iterative evolution but because confusion exists over the early described species where the types have been lost, because dimorphism is highly developed and led in the past to a dual nomenclature and because the detailed measurements required for identification may be precluded by irregularity of individual development.

This inclusive genus is therefore taken to cover flattened discoidal to stoutly lenticular and even globular species with sharp to rounded periphery. The septa are usually curved and the portion overlying previous whorls and usually visible at the surface is called the septal filament. As shown by figure 13.1E – H, the septal filaments may be radial, sigmoid or meandrine and may branch to give a reticulate pattern (incipient chamberlets). The ratio of height to width of the chambers which relates to the tightness of coiling is also considered specific. It is measured in equatorial section as is chamber number per whorl or quadrant. The pattern of pillars may also be specific and they are commonly arranged along septal filaments and/or along the spiral cord or over the poles (umbilical). It should be noted that the last chamber is usually broken because the primary lamella is so thin. The aperture (even if one is developed) is therefore not seen. However, the foramen is a basal slit accompanied by round, areal passages, irregularly placed (stolons of Hottinger, 1977a). Communication with the canal system is established by resorption and creation of passages in the roof of the chambers and through the alar prolongations to the umbilicus.

The second chamber in nummulitids tends to be larger than the third and the amount of overlap has been expressed as 'factor E' and measured in successive populations (Vlerk and Bannink, 1969). Further biometrical studies and attempts at numerical taxonomy have been made by Khan and Drooger (1971), Vlerk *et al.* (1972), Barnett (1974) and Blondeau *et al.* (1977).

ORBITOIDAL TEST ARCHITECTURE

As already discussed, subannular to annular complex test architecture is developed along a number of unrelated lines within the Rotaliida. This culminates in tripartite, 'orbitoidal', structures with an equatorial layer sandwiched between lateral layers of chamberlets on either side (figure 13.2A; plate 13, bottom). The overall shape is generally that of a flattened spheroid, 'flying saucer' shape, but varies from globular to lenticular and is fan shaped in subannular genera. The periphery is usually angular, often produced into a flange and round or stellate in plan view.

The character of the equatorial layer is considered most diagnostic in classification. This is because it records more or less clearly the progressive change from primary planispiral (or trochospiral) growth to annular or concentric growth. The primary planispire may be retained in the microspheric generation, even in advanced forms, but in megalospheric forms becomes reduced to a few chambers (nepion) surrounding

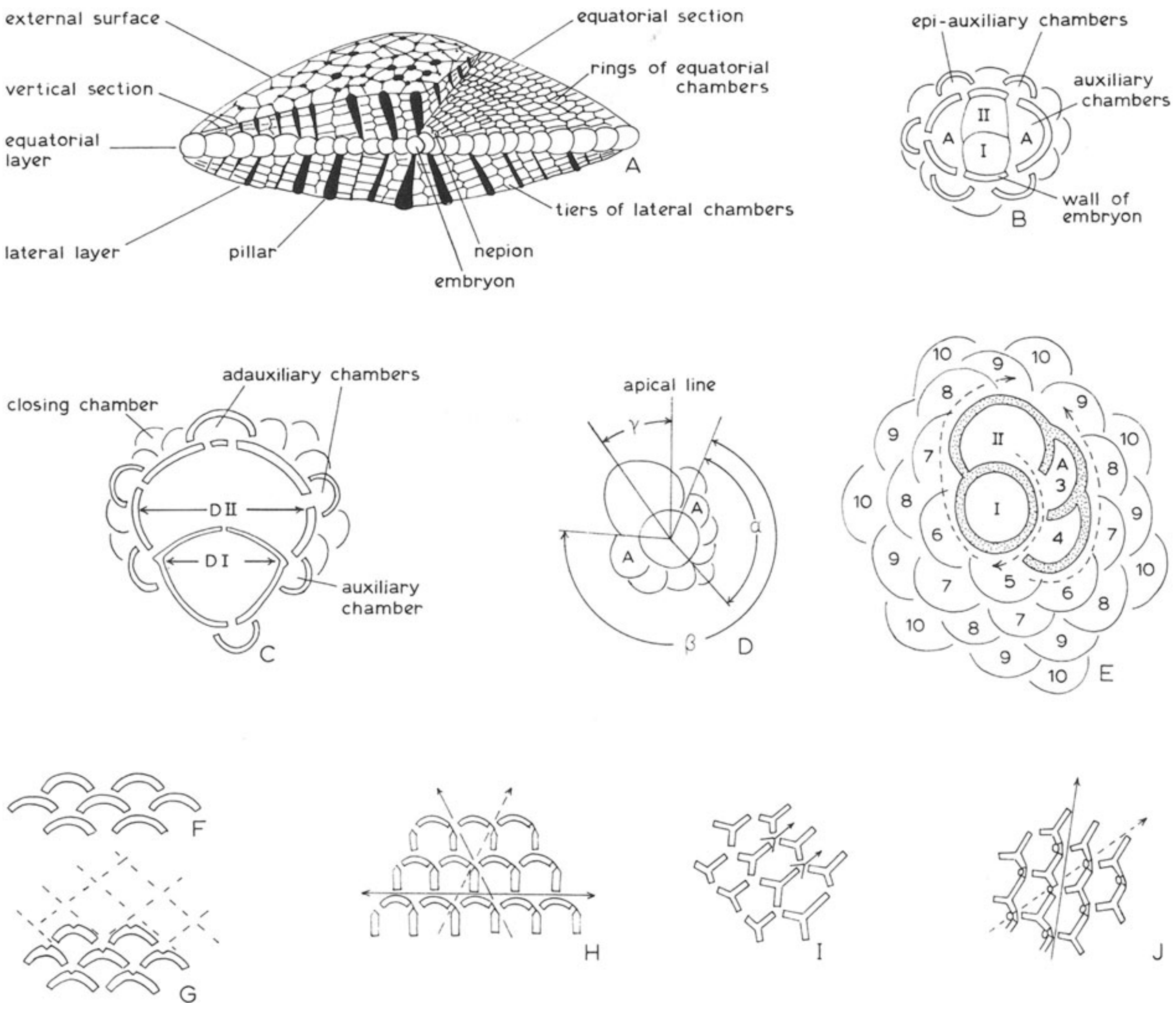


Figure 13.2 Morphology of the orbitoidal test

A Specimen cut-away to show external surface, equatorial section and vertical section

B Quadrilocular embryon of *Orbitoides,* showing included auxiliary chambers and nepion with 5 epi-auxiliary chambers, 2 reduced spirals and closing chambers (auxiliary chambers symmetrical, $X=12$, $Y=2$), after Van Gorsel

C Bilocular embryon of *Lepidocyclina* s.l., showing auxiliary chambers, 4 reduced spirals and closing chambers (deuteroconch symmetrical, $X=14$, $Y=1$, $C=3$), after Van Vessem

D Important measures of the juvenarium of *Miogypsina,* showing bilocular embryon and 2 spirals (deuteroconch symmetrical, $X=8$, $Y=2$, $C=0$), after Raju

E Orbitoid with arcuate chambers, showing how the introduction of symmetrical chambers (chambers with primary aperture only stippled, $Y=4$) at '5th budding stage' leads to the formation of a counterspiral and to rings of chambers by the 10th budding stage, after Van Gorsel

F – J Equatorial chamber(let)s and communications: F simple arcuate chambers with 2 apertures forming 4 stolon systems, as in *Planorbulina* and early orbitoids; G chambers compressed diamond shaped (ogival) with diagonal four-stolon system, giving 'engine-turned' appearance, as in *Miogypsina* and *Omphalocyclus;* H spatulate to hexagonal chambers with crossed over diagonal and annular, six-stolon system, as in advanced orbitoids; I hexagonal chamberlets with Y-shaped stolons, as in certain heterosteginids; J hexagonal chamberlets with crossed over diagonal stolons, as in *Cycloclypeus;* F – H after Van Gorsel, I and J after Hottinger enlarged initial chambers (nucleoconch or embryon). It may be lost altogether in the process of 'nepionic reduction' with acceleration of the incoming of adult chambers. These early chambers are collectively known as the juvenarium (neanic stage) to distinguish them from the adult chambers (ephebic stage).

Although parallel development impresses similar architecture on the orbitoids, the details are different in the different groups and the structures are not homologous. Thus the equatorial layer in the complex nummulitaceans is composed of subannular to annular chambers divided into chamberlets formed by folding of the internal septal flap or divided by radial plates produced from the marginal cord. In the Orbitoididae, it is formed by rings of small, bilamellar chambers like those of *Planorbulina*. Similar arcuate equatorial chambers occur in the complex rotaliaceans such as the Miogypsinidae and Lepidocyclinidae but appear to be modifications of the toothplate.

The embryon is almost always subcentral to central but is at the margin of the equatorial layer in early miogypsinids. It usually consists of two chambers, the proloculus (protoconch) and an enlarged second chamber (deuteroconch). In a number of lines, especially in the Discocyclinidae and Lepidocyclinidae, there is a strong tendency for the deuteroconch to embrace the protoconch. The angle of attachment measured from the centre of the protoconch through the points of attachment of the deuteroconch is expressed as the alpha value and the percentage overlap as the Ai value (Vlerk, 1973). The diameters of the protoconch and deuteroconch, measured at right angles to a line joining their centres, are also considered important, expressed as DI and DII (figure 13.2C). In the Orbitoididae, a further one or two nepionic chambers become incorporated, to form a trilocular or quadrilocular embryon within a thick integument. There are also cases where the deuteroconch is smaller, as in some lepidocyclines. The embryon may consist of a number of irregular chambers. These are usually regarded as sports (teratological) but as examples are quite numerous and include genera at the ends of phyletic lines, such as *Simporbites,* this requires further investigation.

The nepion is apparently variable at the subgeneric and specific level and is therefore less useful at the generic level than the embryon. Appraisal also requires the statistical study of large populations by means of perfectly orientated sections which presents some difficulty and is generally too time consuming for industrial micropalaeontology (Cole, 1957). However, as will be appreciated, such methods are required for study of evolutionary lineages.

Nepionic chambers are distinguished as auxiliary if their walls rest on the embryon, interauxiliary when they are formed from the auxiliary chambers. Auxiliary chambers are primary if they originate over stolons between the protoconch and deuteroconch so that their walls rest on both. There are one or two according to whether there are one or two stolons. Accessory auxiliary chambers arise over stolons in the deuteroconch (adauxiliary) or protoconch (protoconchal) and may reach five or six in number (figure 13.2C). In *Orbitoides,* because the primary auxiliary chambers are incorporated in the embryon, the first nepionic chambers arising above stolons in the embryonic wall are termed epi-auxiliary (figure 13.2B). The formation of the auxiliary chambers is regarded as one 'budding stage' or instar.

The development of the spirals of interauxiliary chambers depends on the number of auxiliary chambers and whether they have only one primary, basal aperture (as in most small rotaliids) or a second, basal aperture at the peripheral margin ('retrovert' as in *Planorbulina*). A chamber with a second, retrovert aperture is termed symmetrical or progressive. In the case of one auxiliary chamber with a single basal aperture, a single (protoconchal) spiral results, terminated eventually by the appearance of a symmetrical 'closing' chamber (figure 13.2E). When there are two apertures the retrovert aperture generates a second (deuteroconchal) counter-spiral. When there are two auxiliary chambers three or four spirals may result. The nepionic spirals may therefore be single, double, treble or quadruple. These spirals usually end when they meet each other, with appearance of another symmetrical chamber linking them. This leads to the appearance of subannular or annular rings of adult chambers, by budding stage ten in the example shown in figure 13.2E.

N.B. Terms such as 'uniserial' and 'biserial' for single and double nepionic spirals should be avoided because of confusion with the terminology for Smaller Foraminifera; so also should 'proximal' and 'distal' for primary and secondary apertures.

Measurements considered important in the appraisal of the nepion include the total number of chambers, expressed as *X;* the number counted to the first symmetrical chamber, expressed as *Y;* the percentage circumference of the embryon covered by auxiliary chambers, expressed as *B;* the total adauxiliary chambers, expressed as *C*. Additional measurements found of particular value in the Miogypsinidae (Drooger, 1952b, 1963) are: alpha, the arc length of the circumference of the protoconch covered by the smallest protoconchal nepionic spiral; beta, the arc length of both larger and smaller protoconchal spirals; gamma, the angle between the line through the centre of the embryon and the line from the protoconch through the middle of the test to the apex (figure 13.2D). The degree of symmetry of the protoconchal spirals is also considered valuable, 200 alpha/beta = *V* (see Amato and Drooger, 1969; Raju, 1974).

The adult stage of the equatorial layer consists of subannular to annular rings of chambers or chamberlets. Their shape varies from rectangular to hexagonal (Nummulitacea), from arcuate to ogival and diamond shaped (Orbitoididae), from arcuate to ogival or arcuate to spatulate and hexagonal (Miogypsinidae, Lepidorbitoididae and Lepidocyclinidae). More than one layer may be developed towards the periphery and multiplication or enlargement in sectors (rays) may lead to a stellate outline.

The development of the stolon system of communication relates to chamber shape in that simple, arcuate chambers possess four stolons derived from the original double apertures, as seen in *Planorbulina* (figure 13.2F,G). Advanced spatulate and hexagonal chambers show a basal or proximal, annular passage as well, which gives a six-stolon system (figure 13.2H). Several sets of superposed diagonal and annular stolons may eventually appear in each chamber. However, variation of the stolon pattern within individual specimens has led some authors, such as Eames *et al.* (1962b) and Van Gorsel (1975, 1978), to doubt their taxonomic usefulness in the Orbitoididae and the Lepidocyclinidae. A practical difficulty is that stolons are usually only seen in well-preserved specimens after infiltration of a coloured matrix and very rarely in vertical section. Proper study requires casts which cannot be made if the system is already infilled. In contrast, as noted above, Hottinger (1977a, 1978) regards the stolon system in members of the Cycloclypeidae as diagnostic at the generic level, an 8-shaped crossover system being achieved in *Cycloclypeus*. The development of annular stolons in the Discocyclinidae is also deemed to be of generic significance by Samanta (1967). They are mostly proximal in *Discocyclina* and *Asterocyclina* and distal in *Pseudophragmina* and *Asterophragmina*.

The lateral chamber(let)s have generally been disregarded in classification, except by Scheffen (1932), although they show progressive development in most lines. Early forms show irregular vacuoles but in advanced forms the chambers are well formed, low polygonal to hexagonal in shape and arranged in overlapping or regular tiers. The corners tend to be thickened as pillars which may develop into large pustules and the sutures may be thickened and raised into a boxwork ornament. In some cases the surface is ornamented with radial ridges. Communication appears to be through coarse pores but stolons have also been described, giving vertical connection with the equatorial layer in *Miogypsina* (Bock, 1976).

The mode of formation of the lateral chambers is not fully understood. If they are formed by buckling of the outer lamellae (Smout, 1954) then each layer can be regarded as a series of chamberlets produced by one instar. This may be the case in the nummulitaceans. If they are formed by folding of both lamellae of the primary wall (Hottinger, 1978), then each layer can be regarded as a series of chambers involving several instars. It is significant that both in the Nummulitacea and in the other groups of orbitoids the number of lateral cycles is nearly always less than those in the equatorial layer. The lateral chambers may not cover the entire surface, thus involute and evolute types of *Orbitoides* can be distinguished, and in many discocyclinids and pseudorbitoidids the edge of the equatorial layer is bare when developed as a flange. This indicates that the development of the equatorial layers and lateral layers is probably not simultaneous. Despite these difficulties, the future diagnostic use of the lateral layers is intimated by Van Gorsel's view that within the *Orbitoides* lineage, 'the degree of development is a good indication of evolutionary stage'.

POSSIBLE EVOLUTIONARY RELATIONSHIPS

Modern work largely confirms the view of Glaessner (1945, see reprint 1963a) that the large rotaliids were derived along a number of separate lines from different families of small rotaliids. *Rotalia* appeared in the Upper Cretaceous, possibly from among the Discorbidae, and rapidly gave rise to the different families of the Rotaliacea. The mainly, low conical members of the Rotaliidae appear in the early Palaeogene, including *Dictyokathina* in the late Palaeocene and *Dictyoconoides* in the Middle Eocene, while the complex, high conical Chapmaninidae appear in the late Palaeogene and Middle Tertiary. *Rotalia* gave rise to both the Calcarinidae, via *R. calcar,* and the Miscellaneidae, possibly via the asymmetric *Storssella,* in the Upper Cretaceous. *Calcarina* and *Siderolites* are present in the Upper Cretaceous, *Baculogypsinoides* by the Eocene, but the advanced *Baculogypsina* not until Neogene.

Two major groups of subannular or annular complex genera arose within the Rotaliacea, the *Lepidorbitoididae* from *Pseudosiderolites* (Miscellaneidae) via *Helicorbitoides* in the late Cretaceous (Gorsel, 1975) and the Miogypsinidae, again from *Rotalia* (*Pararotalia*) via *Miogypsinoides* in the uppermost Oligocene (Tan Sin Hok, 1936a; Barker and Grimsdale, 1937).

The earliest member of the Nummulitacea may be *Sulcoperculina* which appears to have arisen from among the Miscellaneidae in the Upper Cretaceous. Both *Nummulites* and *Operculina* are present in the late Palaeocene and together with *Ranikothalia* which is abundant at the Palaeocene/Eocene boundary may have descended from a common ancestor, questionably *Sulcoperculina* (Arni, 1966).

Annular complex forms appeared remarkably quickly in this superfamily, the Pseudorbitoididae springing directly from *Sulcoperculina* via *Sulcorbitoides* in the late Cretaceous. The Cycloclypeidae appear to be polyphyletic and heterosteginids have arisen at least twice from operculine stocks (Tan Sin Hok, 1939; Papp and Küpper, 1954; Papp, 1963; Herb, 1978) in the Eocene and Miocene. At least eight lineages are claimed for the *Cycloclypeus* group (MacGillavry, 1962). A feature of this group is the dominance of subannular to annular discoid growth with subannular complex architecture achieved only once in *Spiroclypeus* which appeared in the Eocene directly from *Heterostegina* and does not range above the L. Miocene. On the face of it, their natural culmination might appear to be in the discocyclinids which show advanced annular complex structure with rectangular to hexagonal equatorial chamberlets and almost completely reduced nepion. But this family arose earlier, in the Palaeocene, and died out at the end of the Eocene. It is also distinguished by a large, embracing, bilocular embryon.

Vaughan (1945) suggested that the Discocyclinidae evolved from an early nummulitid but Brönnimann (1951) disputed the presence of true canals (apparently seen in *D. pratti,* see key figure 13.10) and regarded these structures as open fissures, like those in the Rotaliacea. Samanta (1967) similarly regards the resemblances to nummulitids as superficial. The possibility of a rotaliacean origin suggests a connection with *Lepidorbitoides* (MacGillavry, 1963) which also has a bilocular embryon, or with the 'enigmatic' *Orbitoclypeus* group which Gorsel (1978) regards as a lineage separate from the Lepidorbitoididae and possibly derived from the nummulitid, *Sulcoperculina.* However, the presence of a *Cycloclypeus*-like initial part in microspheric forms of *Discocyclina* (Brönniman, 1945; Neumann, 1958; Caudri, 1972) seems to rule out these ideas.

The origin of the Orbitoididae has aroused much dispute, depending on different interpretations of the microspheric juvenarium. Thus Küpper (1954), followed by MacGillavry (1963) and Van Hinte (1965), regards the initial chambers in *Orbitoides* and *Omphalocyclus* as biserial, suggesting a heterohelicid ancestor like *Planoglobulina* with biserial initial stage followed by cyclical growth. It was further supposed that the embryon might be planktonic, which would explain the wide distribution of these genera. In contradiction, Neumann (1958) and Hofker (1958, 1963) regard the initial chambers as spiral then irregular. Hofker explains the apparent biserial mode seen by other workers as a false impression due to the plane of sectioning. He prefers *Dyocibicides* as an ancestor, although this genus is not known before the Tertiary. Taking all these views into account, Van Gorsel (1978) interprets the microspheric juvenarium as spiral, becoming irregularly alternate. He notes that spiral initial chambers only occur in the microspheric generation of most heterohelicids; that the equatorial chambers of early *Orbitoides* species are acervuline, suggestive of an attached mode of life; and that wide distribution could be due to rafting of the juveniles. He therefore supports the idea of derivation from an, as yet unknown, *Dyocibicides.* On balance, therefore, this family of non-canaliculate orbitoids probably arose from a *Planorbulina*-like member of the *Cibicides* group in the late Cretaceous.

The origin of the Lepidocyclinidae is less controversial. Barker and Grimsdale (1936) and Grimsdale (1959) have demonstrated that this family arose from *Amphistegina* via *Helicostegina* in the early Middle Eocene, leading to *Polylepidina* (= *Eulinderina*) and *Helicolepidina.* Two lineages distinguished by crossed over and uncrossed stolons were recognised.

ADAPTIVE TRENDS

As outlined above, the major morphological trends exhibited by the large rotaliids can be considered progressive solutions to the problems of a life strategy which exploits the possibilities of symbiosis. This necessarily takes place within the 'structural confines' (MacGillavry, 1978) of the calcareous, lamellar test and in the turbulent photic zone, which explains the striking, parallel development of so many lines.

The trends which have become recognised as general since the brilliant pioneer studies of Vlerk (1922) and Tan Sin Hok (1932) include:

(1) A pervasive tendency to an increase in size of the test, together with an increase in size of the embryon, especially the deuteroconch in orbitoids which tends to become more embracing.

The very large sizes achieved, especially in the Nummulitacea, reflect the high growth rates that can be sustained by symbiotic species in warm, tropical waters. According to Ross (1977). Recent tropical species commonly exceed 15 mm diameter and 200 mm^3 volume in two years' growth, a rate which is 50 – 100 times that of small, temperate species. Increased size can be considered to give a simple, selective advantage according to Cope's rule (Gorsel, 1978), and there may be an advantage in reaching a critical volume as soon as possible (*Q* factor of Drooger, 1974) and an increase in size of the embryon may speed up this process (Hinte, 1965). However, the general increase in size of the embryon is not constant. Fluctuations of as much as 25 per cent occur in successive assemblages of lepidocyclines (Vessem, 1978) and the protoconch has been found variable in size in both *Lepidorbitoides* (Gorsel, 1975) and in the Miogypsinidae (Drooger and Raju, 1973). Large-sized protoconchs were considered to be related to high light intensity in the photic zone and small sized ones to greater depth and also to the effect of the introduction of lateral chambers; although note that this tendency to a smaller size at greater depth will be counteracted by the tendency towards the large size of slower growing specimens at depth and known in *Operculina* (Chaproniere, 1975; Fermont, 1977).

(2) A tendency towards an increase in number of the chambers, introduction of intercalated whorls, subdivision of chambers and the introduction of progressive auxiliary chambers with retrovert apertures which leads to annular growth.

These developments not only solve certain architectural problems, as mentioned earlier, but facilitate higher growth rates, especially in annular genera in which the chamber(s) can be secreted simultaneously all round the periphery.

(3) A tendency towards radial symmetry, brought about by annular growth, the move of the embryon to the centre and the introduction of radial, stolon passages.

By this means shorter communications between the centre and the periphery are achieved and more efficient internal organisation (Hinte, 1965; Gorsel, 1978). It is probably closely related to the more sedentary life possible for symbiotic forms (Chaproniere, 1975). Where the spire is retained, as in large members of the Rotaliidae and Nummulitidae, a similar result is obtained by introduction of radial canals that pierce the spiral wall.

(4) Acceleration of the incoming of adult characters with concomitant reduction and suppression of the ancestral spire (nepionic reduction) in orbitoids, considered by MacGillavry (1963) following Tan Sin Hok (1932, 1936a, 1936b, 1937) as the most important trend.

Evolutionary development by appearance of new features in the adult ('deuterogenetic mode') with gradual restriction of earlier chamber arrangement and form to the juvenile of the microspheric generation, before final disappearance, is general in the Foraminifera, as explained earlier. The effects of nepionic reduction are spectacular in orbitoids because it is combined with differentiation of the juvenarium (nepionic acceleration) including increased size of the embryon and increase in numbers of auxiliary, nepionic chambers, especially adauxiliary chambers in lepidocyclines and epi-auxiliary chambers in orbitoidids. As noted earlier, the main types of development are determined according to whether the adult, equatorial layer is formed of annular chambers subdivided into chamberlets, rings of modified primary chambers with extra aperture as in *Caribbeaneila* and *Planorbulina,* or secondary chambers formed from toothplates or other internal structures—although there are probably as many types as there are ancestral genera.

Ephebic acceleration and attendant nepionic reduction proceeded at different rates in different lineages. A particular feature of the Lepidorbitoididae and the Lepidocyclinidae is the persistence of the primary spiral in the megalospheric generation of early species, described by Van Gorsel (1975) as 'an unrolling spiral of large chambers' with smaller progressive, equatorial chambers forming at a slower rate between the whorls. The subannular growth of *Miogypsina* is similar (Drooger, 1974) but the equatorial chambers are added constantly along the same sector of the periphery. A peculiarity of the Pseudorbitoididae (Brönnimann, 1955a) is that equatorial chamberlets may be absent in all but the most advanced species, so that the characteristic plates rest directly upon the lateral layers. However, this is disputed by MacGillavry (1963) and Krijnen (1972) who claim that arcuate equatorial chambers are present. Annular chambers are only achieved in the outer part of the equatorial layer of the most advanced genus, *Vaughanina.*

MacGillavry (1978) regards nepionic reduction as a gradational, directional trend, with shift of the mode through successive assemblages, that cannot be reconciled very easily with allopatric speciation; indeed, Tan Sin Hok (1932) concluded that it took place independently of external selective factors. Eldredge and Gould (1972) believe such gradual changes 'hardly ever' occur, which has led MacGillavry to suggest the mechanism of 'clone selection' which apparently can occur in environments with low faunal diversity producing the 'pseudo-gradualism' of Gould and Eldredge (1977).

(5) The tendency for the equatorial chamber(let)s in advanced forms to become ogival (diamond shaped) or hexagonal (prisms).

The development of hexagonal chambers is particularly well seen in the Cycloclypeidae, the Lepidorbitoididae, in some lineages of the Lepidocyclinidae and Miogypsinidae and also, to some degree, even in the Discocyclinidae. It represents the response to the need for the most efficient packing, seen in so many animal and plant structures. As already noted, it is accompanied by the development of the six-stolon system and crossed over communication. In *Orbitoides,* in contrast, where the chambers remain arcuate, the equatorial layer compensates by greater thickness. Advanced orbitoidids, most of the Miogypsinidae and some lines of Lepidocyclinidae develop ogival chambers, together with the diagonal, four-stolon system.

(6) The progressive differentiation of lateral chamber(let)s which become well developed in advanced forms.

As discussed, this development solves the architectural problem of the build-up of lateral lamellae at the same time as providing ideal housing for algae (Grimsdale, 1959; Drooger and Raju, 1973). It is significant that there is only one example of annular complex growth, *Spiroclypeus,* in the Cycloclypeidae which spring from nummulitids which tend to develop a marginal cord and keep the sides thin. Also that the large, low conical members of the Rotaliidae, such as *Dictyoconoides,* do build up a thick crust of lamellae on the ventral side, possibly as a protective device in very shallow waters with very strong light.

The introduction of lateral chambers allows the appearance of symmetrical growth and the spherical shape which is 'most efficient' (Smout, 1954) and best adapted to reefal and high energy conditions (Haynes, 1965). However, as previously discussed, most orbitoids and nummulitids are flattened and do not reach this ideal. The calcarinids which do achieve sphericity also develop spines for lodgement in reefal conditions and the most spherical species of *Nummulites,* such as *N. globulus,* have the thickest walls and massive umbonal plugs for support. Where currents are less strong, and also at greater depths where light for photosynthesis becomes reduced, a higher surface to volume ratio and flattened form becomes an advantage for symbiosis. Studies of modern rotaliids confirm that there is a definite relation of shape to depth (Hottinger and Dreher, 1974; Larsen, 1976; Hottinger, 1977b; Larsen and Drooger, 1977) with 'decreasing test oblateness with increasing depth' (Hallock, 1979). Also, many large rotaliids remained distinctly asymmetric in plan. Thus most miogypsinids are fan shaped, with the embryon near the periphery, which may have had an advantage in allowing orientation to currents, or even a vertical habit. The asymmetric operculines and heterosteginids may also have stuck obliquely or vertically out of the sediment and are known to crawl up elevated points of the substrate (fossil evidence—Haynes, 1962; observations on living forms—Lutze *et al.,* 1971; Ross, 1972; Hottinger, 1977b). The marked rim or flange developed in many orbitoids, even when subspherical in shape, may have served to spread out the network of pseudopods, like the keel in *Amphistegina,* as observed by Banner (1978), or supported an ectoplasmic sheath.

ECOLOGY

Investigations into the ecology and distribution of living representatives of the large Rotaliidae have been made both in the Red Sea (Gulf of Elat) by Reiss *et al.* (1977) and by Pamela Hallock in the Pacific (1979). This includes information on *Amphistegina* (which was ancestral to the lepidocyclines), *Baculogypsina, Calcarina, Operculina* and *Heterostegina* (inc. *Heterocyclina*). As shown by Hottinger's contribution to the Red Sea study, the distributions coincide closely with depth contours and substrate:

Heterostegina compressa	20 – 70 m, hard bottoms.
H. depressa	40 – 75 m, hard bottoms.
Heterocyclina tuberculata	70 – 150 m, soft bottoms.
Operculina ammonoides	30 – 150 m, soft bottoms.

Individual specimens tend to be flat or at an angle to the substrate or even sticking to roots of *Halophila* and most closely orientated to available light on soft bottoms. They also tend to cluster. Significantly, specimens of *O. ammonoides* below 70 m are mainly dead juveniles without symbionts and large peneroplids are dominant above 20 m depth. As noted above, in the section on adaptive trends, these large rotaliids (and *Amphistegina* studied by Larsen and Drooger) become more evolute and compressed with depth. An interesting observation made by Hottinger is that large Foraminifera are commonly transported in drifting clouds of filamentous green algae by currents parallel to the coast.

Pamela Hallock has studied the distribution of 15 species around the Caroline Islands and Hawaii, including *Amphistegina, Baculogypsina, Calcarina, Operculina* and *Heterostegina*. Her results are important for application in palaeo-ecology in that: very rotund species (*B. sphaerulata* and *C. spengleri*) are only abundant at depths less than 10 m and are restricted to reef flats and turbulent areas; *A. lessonii* with intermediate sphericity dominates between 5 and 20 m depth; flatter species are seldom abundant above 15 m depth but extend to the limits of the photic zone. The numbers of *H. depressa* tend to be low in shallow water and restricted to shaded locations. She concludes (cf. Haynes, 1965) 'that both water motion and light interact to influence test shape in symbiont bearing foraminifera'.

These results add precision to palaeo-ecological determinations based on the general assumption that the presence of large Foraminifera indicates the inner shelf and photic zone. In particular it suggests that the typical annular complex orbitoid with intermediate sphericities (thickness/diameter ratios 0.35 – 0.65) occupied intermediate depths in the photic zone and supports conclusions already reached on general grounds. For instance, Gorsel (1978) regards 50 m as the limit for most genera. He notes that *Orbitoides* and *Vaughanina* occur at many localities in sediments regarded as back-reefal and probably in shallower water than *Lepidorbitoides*. *Pseudorbitoides* is 'hardly ever' found associated with other orbitoids and is believed to indicate a relatively deep fore-reef environment in the Cretaceous of the Caribbean area. Raju (1974) concludes that all available evidence from the associated biota and sediment suggests that the Miogypsinidae lived in shallow marine environments with frequent high energy conditions and only rarely in deeper, or at least quieter, marine environments. Strongly undulated tests seem to be related to soft bottoms.

A particularly interesting piece of work in which associations of large rotaliids are applied in palaeo-ecology with a high degree of precision, is that by Chaproniere (1975), on the Oligo-Miocene of the Northwest Cape area of Western Australia. Eight associations, including some porcelaneous genera, are recognised representing the following environments:

Shallow marine (less than 12 m depth) sea grass communities—

(1) sheltered—*Lepidocyclina (Eulepidina) ephippioides/Heterostegina borneensis,*
(2) open—*L. (Nephrolepidina) howchini/Cycloclypeus eidae—carpenteri,*
(3) metahaline (salinities 40 – 56 per thousand) —*L. (N)howchini/Marginopora vertebralis.*

Shallow (less than 30 m depth) high energy sands—

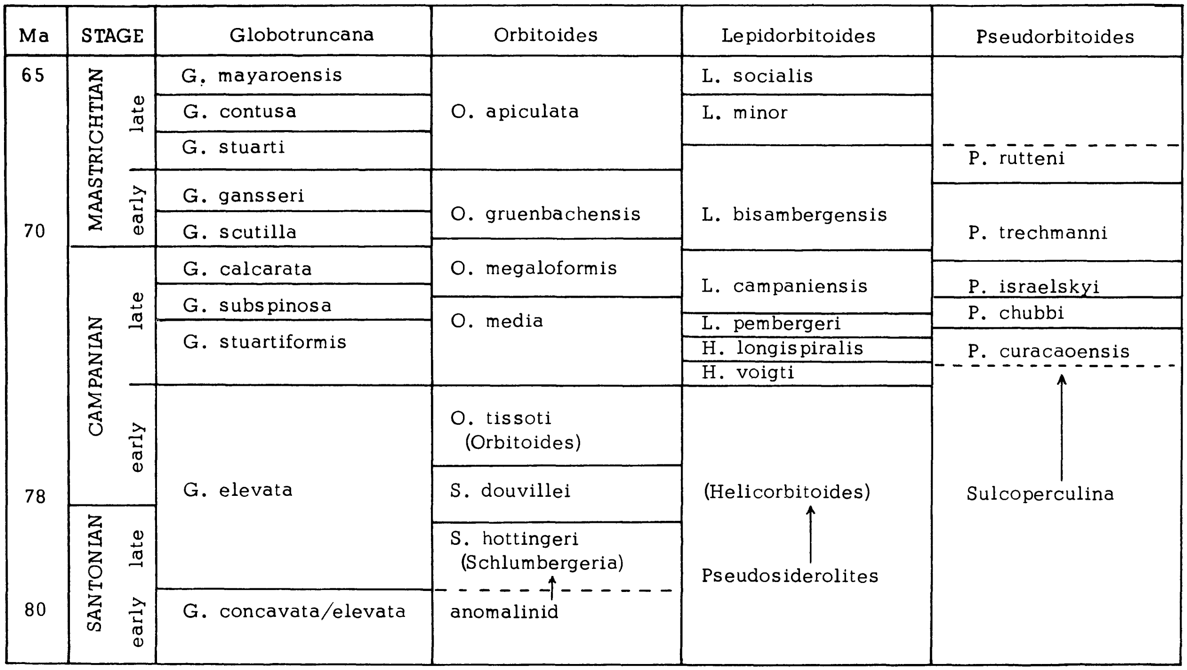
(4) normal marine—*Operculina complanata/Gypsina howchini,*
(5) metahaline—*Austrotrillina howchini/Flosculinella bontangensis.*

Open marine, low energy (greater than 12 m depth)—

(6) intermediate photic zone—*L.(E.) badjirraensis/C.eidae,*
(7) intermediate photic zone to 120 m —*C.eidae/O.complanata,*
(8) below photic zone (+ 120 m)—*O.complanata*/small benthonics.

APPLICATION IN STRATIGRAPHY

The rapid evolution of the large Rotaliidae means that this group provides some of the most valuable index fossils, in a number of cases at the generic and even at the family level (figures 13.3 to 13.6). The Cretaceous families of orbitoids all appeared in the late Senonian and became extinct during the



Ma	STAGE		Globotruncana	Orbitoides	Lepidorbitoides	Pseudorbitoides
65	MAASTRICHTIAN	late	G. mayaroensis	O. apiculata	L. socialis	
			G. contusa		L. minor	
			G. stuarti			P. rutteni
		early	G. gansseri	O. gruenbachensis	L. bisambergensis	
70			G. scutilla			P. trechmanni
	CAMPANIAN	late	G. calcarata	O. megaloformis	L. campaniensis	
			G. subspinosa	O. media	L. pembergeri	P. israelskyi P. chubbi
			G. stuartiformis		H. longispiralis H. voigti	P. curacaoensis
		early	G. elevata	O. tissoti (Orbitoides)		↑
78				S. douvillei	(Helicorbitoides)	Sulcoperculina
	SANTONIAN	late		S. hottingeri (Schlumbergeria) ↑	↑ Pseudosiderolites	
80		early	G. concavata/elevata	anomalinid		

Figure 13.3 Some important lineages of Upper Cretaceous orbitoids with range zones tentatively correlated with the planktonic foram zones and the radiometric dates. After Gorsel (1978) and based on various authors

Maastrichtian or at its close with only doubtful records in the Palaeocene. *Omphalocyclus* is apparently restricted to the Maastrichtian. The early Palaeocene interregnum was followed by the appearance of *Nummulites* and *Discocyclina* in the late Middle Palaeocene. The Discocyclinidae became extinct at the end of the Eocene and *Nummulites* s.s. towards the end of the Oligocene. *Asterocyclina* is restricted to the Middle and Upper Eocene. The Lepidocyclinidae appeared in the Middle Eocene and the Miogypsinidae in the late Oligocene, both families becoming extinct at the end of the Middle Miocene or early Upper Miocene. *Miogypsinoides* ranges from the Upper Oligocene to the early Middle Miocene and *Miogypsina* is restricted to the Lower and Middle Miocene. In contrast, the Cycloclypeidae range from the Eocene down to the Recent but *Spiroclypeus* became extinct in the early Lower Miocene.

The attempt to refine biostratigraphical application by close analysis of lineages began at an early date. In the case of the Cretaceous orbitoids the evolutionary sequence, *Orbitoides tissoti* through *O. media* to *O. apiculata,* was first recognised by Douvillé (1915, 1920) and has since received much attention (Küpper, 1954; Papp, 1956; Neumann, 1958, 1972, 1973; MacGillavry, 1963; Hinte, 1965, 1966a, 1966b; Gorsel, 1978). The Orbitoididae are now considered to represent one lineage of seven species stemming from *O. hottingeri* (= *Schumbergeria*) in the late Santonian. Similar work has been carried out on the Lepidorbitoididae (Papp and Küpper, 1953a, 1953b, 1953c; Papp 1956; Gorsel, 1975). This group is again considered one lineage of seven species springing from *Helicorbitoides voighti* in the late Campanian, possibly directly from *Pseudosiderolites.* The Pseudorbitoididae have been studied by Brönnimann (1954–58), MacGillavry (1963), Krijnen (1971, 1972) and Gorsel (1978). This family appears to comprise two lineages, both springing from *Sulcoperculina* in the late Campanian and leading separately to *Pseudorbitoides* and *Vaughanina.* The fine zonation possible when the ranges of the species in these lineages are calibrated with the planktonic foram zones is shown in figure 13.3.

Lineages were recognised earliest of all in *Nummulites,* and Boussac (1911a, 1911b) distinguished three:

(1) Smooth species with radial septa.

(2) Smooth to granulate species (with pillars) and septa meandrine.

(3) Granulate species with radial to reticulate septa.

Douvillé (1906a, 1906b, 1919) also recognised three main groups but changes in septal form and

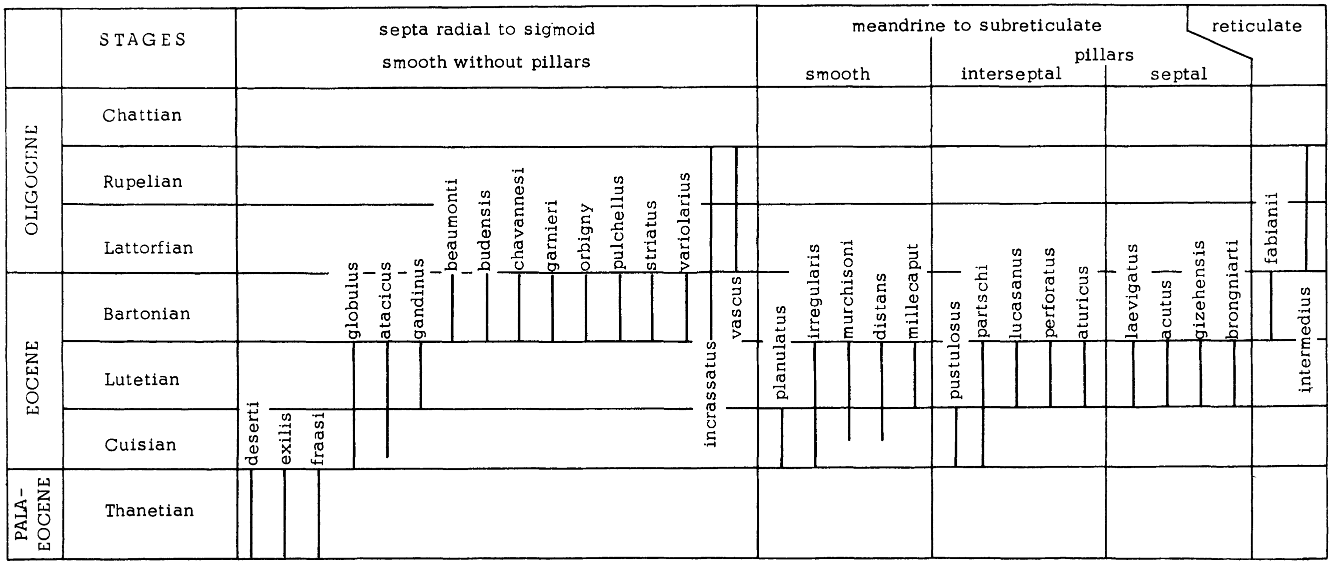


Figure 13.4 General ranges of the chief species groups of *Nummulites* in Western Tethys and Europe. Modified from Eames (1971)

STAGES	Miogypsinoides	Miogypsina	Lepidosemicyclina	INDIAN ZONES
BURDIGALIAN		M. cushman/antillea		antillea
		M. intermedia		
		↑	L. excentrica	excentrica
			L. droogeri	droogeri
	M. indica	M. globulina →	L. thecidaeformis	thecidaeformis
AQUITANIAN	M. dehaartii	M. tani		tani
	M. bantamensis →	M. gunteri		gunteri
CHATTIAN	M. formosensis			
	M. complanata			complanata
	M. cf. bermudezi			(cf. bermudezi)

Figure 13.5 Evolutionary lines in the Indo-Pacific miogypsinids and Indian range zones. Note that the *Lepidosemicyclina* line includes the only miogypsinids to develop hexagonal chambers. After Raju (1974)

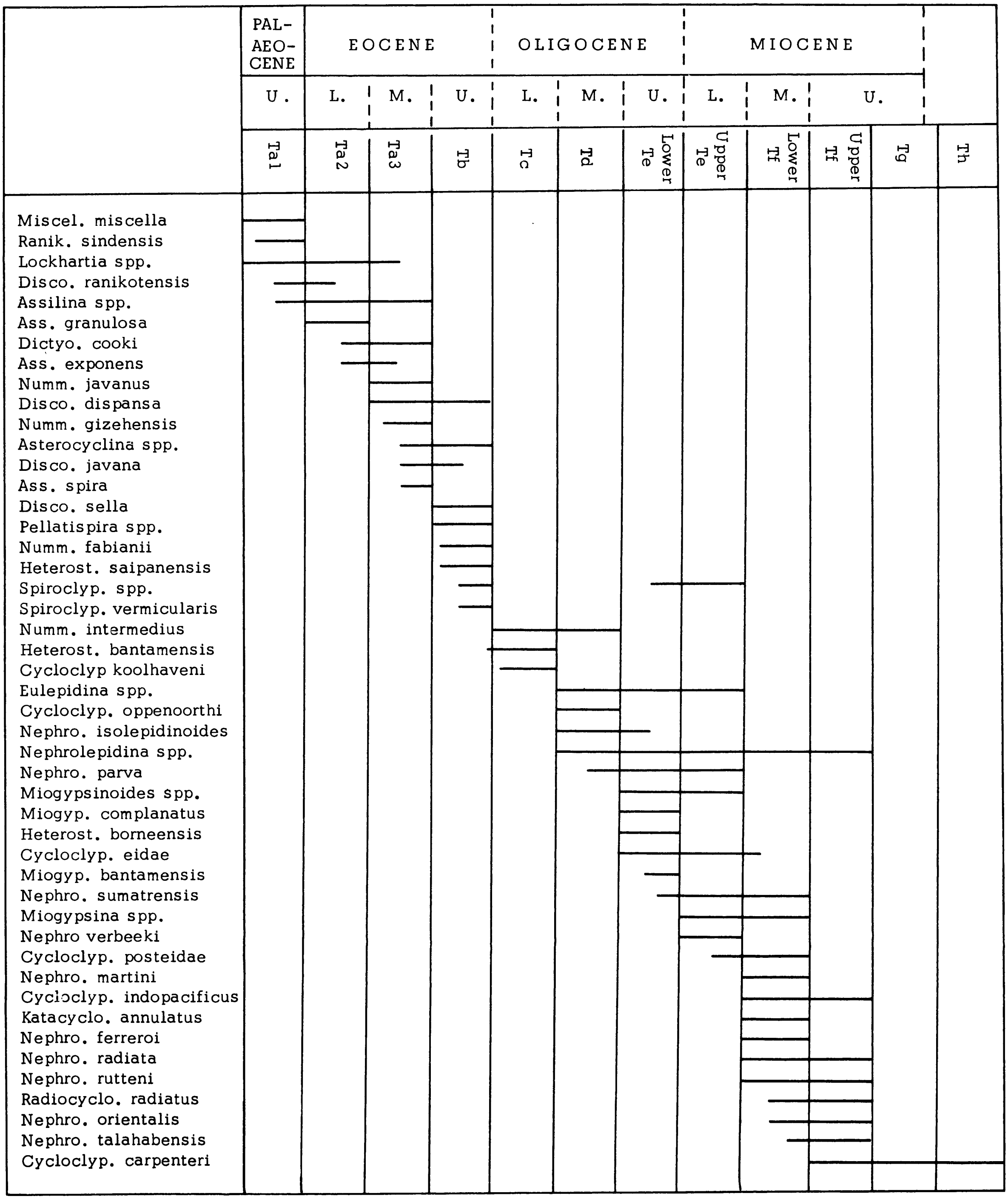


Figure 13.6 Ranges of selected genera of large rotaliids in the Far East. From Adams (1970)

the development of pillars were considered to take place along a number of lines. Some years later, three major principles of evolution in *Nummulites* were propounded by Abrard (1928) who supposed that:

(1) Coiling is from lax and irregular to tight and regular with chambers changing from high and short to low and long.

(2) All lines begin with smooth surface and either remain smooth or develop pillars.

(3) All lines begin with lenticular shapes and become flat or globose.

These ideas were developed further in the evolutionary schemes brought out by Morley Davies (1935) and Glaessner (1945, see reprint 1963a), and especially by Schaub (1951, 1963, 1966) who has recognised two lineages in *Assilina* and six in *Nummulites*. However, Eames (1971) in his revision of Morley Davies's work has abandoned the attempt to distinguish lineages, largely because of changes in the known ranges of many of the species, which means that many of them cannot now be considered ancestral to others, and also because some species in different lines may be synonymous. Schaub's work on the *Nummulites* is, so far, restricted to the Lower and Middle Eocene, so it seems that for the time being they must still be applied as empirical index fossils. Nevertheless, the great value of the successive associations of *Nummulites* species in the Tethyan region is brought out by figure 13.4. It will be seen that the Palaeocene species are small, smooth and have radial to slightly sigmoidal septa. Lower Eocene species show a marked increase in size and include smooth forms with radial to sigmoidal septa and also species with meandrine septa and pillars between or on the septal filaments. The genus appears to reach its acme of development in the Middle Eocene with very large species present such as *N. millecaput* and *N. gizehensis*. Most species have meandrine septa and are smooth or with pillars between the filaments, often following the spire. A number become subreticulate. In the Upper Eocene there is a dramatic fall in size and smooth species with radial to sigmoidal septa again dominate the faunas although small, reticulate species such as *N. fabianii* make their appearance here. Relatively small, smooth species with radial to sigmoid filaments continue through the Lower and Middle Oligocene and are joined by a large, reticulate species, *N. intermedius*, which is characteristic of this interval. It seems clear that this is another example of a polyphyletic group in which larger, more complex forms have arisen many times from small, simple species such as *Nummulites deserti*.

The difficulties in using the typical Tethyan species outside the subtropical palaeolatitudes of their origin has been pointed out in chapter 12. They first enter the North-west European Basin, with the appearance of *N. planulatus*, during the Cuisian as world climates moved towards their Tertiary optimum and are relatively well represented in the Lutetian in warm, clear-water carbonate facies, including *N. laevigatus*, *N. lamarcki* and *N. gandinus*. Drooger *et. al.* (1971) consider that the small radiate nummulites of North-west Europe represent separate lines of development from *N. gandinus*. During the Bartonian this species apparently gave rise to *N. variolarius* in the Paris Basin (? as in Tethys) but to *N. prestwichianus* and in turn *N. rectus* in the Hampshire Basin, and to *N. orbignyi* in the North Sea Basin. In the Oligocene, *N. orbignyi* gave rise finally to *N. germanicus*. Obviously, these evolutionary developments at the periphery of the range of the genus are only of local correlative value.

Vlerk and Bannink (1969) attempted to establish the relative age of nummulite assemblages by assuming progressive change in 'Factor E' (less enclosure of the second chamber by the third with time). However, the difficulties encountered by Whittaker and Hodgkinson (1979) indicate that the method must be applied to single lineages and adaptation to different depths allowed for, as noted above.

Very early in this century, Douvillé (1905) correlated a succession of strata in Borneo with six European stages, from Lutetian to Burdigalian, using the occurrence of large rotaliids. Although the use of European stage names was dropped in the Far East and replaced by the famous 'Letter classification' (Vlerk, 1922; Vlerk and Umbgrove, 1927; Vlerk, 1955, 1959a), the successive assemblages of large rotaliids remained the basis of recognition of the intervals. The whole scheme has recently been re-evaluated and improved by Adams (1970). Difficulties that remain include the lack of sufficiently studied continuous sections that cover stage boundaries, the geographical restriction of many species and lack of calibration with the worldwide, planktonic, foram zones.

In his 1922 paper, Vlerk had already suggested the probable value of evolutionary studies in genera such as *Cycloclypeus* (although this again demands study through continuous sections) and pioneer work on nepionic reduction in this genus was carried out by Tan Sin Hok (1932). Subsequently, *Cycloclypeus* has also been studied by MacGillavry (1956, 1962) and other cycloclypeids by Papp (1963), Hottinger (1977b) and Herb (1978).

Nepionic reduction in *Cycloclypeus* apparently occurs at a steady rate with time, the rate of change being 7.5 per cent per million years according to MacGillavry (1978), which is similar to the rate of change in horse dentition. But straightforward application in stratigraphy is complicated by the existence of at least eight lineages, some of which spring directly from *Heterostegina* and some possibly being branch lines. As these lineages arose at different times and evolved at different rates, MacGillavry stresses that care must be taken to confine analysis to one lineage at a time and also to include a study of other evolving features, if 'Tan's method' is to be applied in stratigraphy successfully.

A further difficulty in the case of *Cycloclypeus* is its absence from America. However, evolutionary studies were rapidly extended to the lepidocyclines which originated in that hemisphere (Tan Sin Hok, 1936b; Barker and Grimsdale, 1936; Grimsdale, 1959; Vlerk, 1955, 1957, 1959a, 1959b, 1963, 1966, 1968, 1973, 1974; Eames *et al.*, 1962b; Drooger and Freudenthal, 1964; Matsamuru, 1971; Meulenkamp and Amato, 1972; Mulder, 1975; Ho Kiam Fui, 1976; Vessem, 1978).

Lepidocyclina originated in the early Middle Eocene, as explained above, and during the rest of the Eocene was only common in the Caribbean area. European and Indo-Pacific lepidocyclines are thought to have been derived from the American stock. An eastward migration along Tethys is thought most likely because species appear first in western Tethys in the Upper Eocene, while *Nephrolepidina* and *Eulepidina* appear together in the Far East in the Middle Oligocene. Van der Vlerk considered there was only one lineage, characterised by the well-known, embryonic acceleration with increase in embracement by the deuteroconch, Ai and nepionic acceleration with increase in adauxiliary chambers, *C*. However, his attempt to apply this as a formula in biostratigraphy has been contested by Eames (1971), who considers that the use of the juvenarium alone in diagnosis and biostratigraphy leads to 'queer conclusions' and that it should be combined with other evidence. Vessem (1978) now believes that *Eulepidina* represents a lineage separate from the main *Lepidocyclina* to *Nephrolepidina* lineage. In addition, there are two groups of Indo-Pacific species *Nephrolepidina*. The main line was possibly derived from the European *N. praemarginata/morgani* gr., and shows time dependent changes through five species from *N. isolepidinoides* to *N. rutteni*. The second group of species which are all lumped in *N. transiens* is probably polyphyletic and does not show sustained change. The Neogene development of these lepidocyclines after their migration route from western Tethys was closed, was different from that of the European representatives. They show smaller embryons but more advanced embryonic acceleration at comparable *C* levels. This gives point to the arguments of Adams (1970) and Eames (1971) and, as in the case of *Cycloclypeus,* means that attention must be confined to one lineage and as many evolutionary features as possibly taken into account, together with calibration against the planktonic foraminiferal zones.

Because they straddle the Palaeogene/Neogene boundary like the lepidocyclines but have a shorter range, the Miogypsinidae are particularly valuable in mid-Tertiary stratigraphy. However, their use has been hampered by the large number of species recognised, over 50, and the failure of authors to agree on their limits. Thus, Cole (1964, 1967) reduced the American species to three only, whereas Hanzawa (1957, 1962) recognised 46 in the western Pacific alone. Workers such as Adams (1965, 1970, 1973) have tried to find a middle way between the 'Charybdis of undue lumping and the Scylla of extreme splitting'.

The pioneer attempt to reduce confusion by plotting out the ontogenetic stages so that the species can be placed in an orderly, evolutionary array was again made by Tan Sin Hok (1936a, 1937) and Barker and Grimsdale (1936), followed by Brönnimann (1940), Drooger (1952b – 1974), Mohan (1958), Souaya (1961), Ujiié (1973), Matsumaru (1973), Drooger and Raju (1973) and Raju (1974). Tan Sin Hok recognised five fundamental types of nepion and a large number of species on the assumption that several could occur in one sample. This approach was modified by Drooger who regards the individuals in one sample as belonging to one, homogeneous population unless discontinuous variation can be proved by means of the measurements outlined earlier in this chapter. The danger here is that, as argued by Eames in the case of the lepidocyclines, other specific features may be missed by undue concentration upon the juvenarium. However, Drooger's results do show progressive nepionic acceleration with time. They also appeared favourable in that they indicated that the miogypsinids belonged to one main stock that he considered kept in touch around the world, although sidelines did develop. The importance of

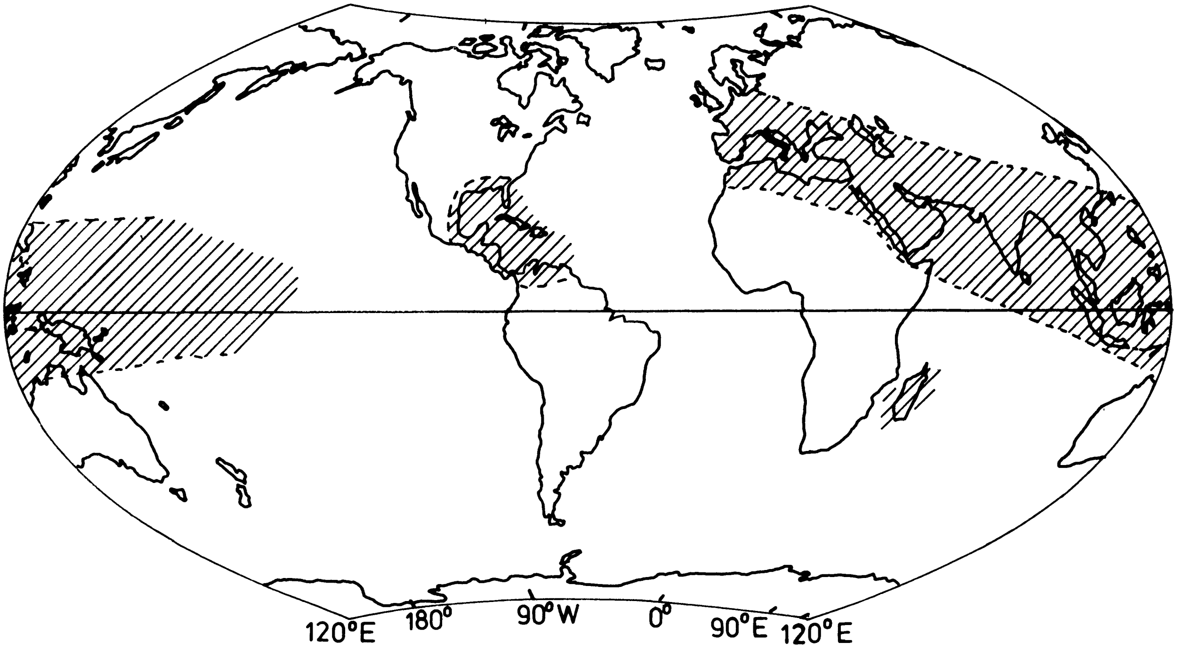


Figure 13.7 Present distribution of the late Cretaceous orbitoidids. After Dilley (1973) and Gorsel (1978)

these sidelines is demonstrated by the work of Raju (1974) in India. This reveals, as shown by the diagram (figure 13.5), that *Miogypsina* s.s. and *Lepidosemicyclina* represent successive branch lines from the *Miogypsinoides* stock, *Miogypsina gunteri* springing from *Miogypsinoides bantamensis* and *Lepidosemicyclina thecidaeformis* from *Miogypsina globulina*. The later *Miogypsinoides* species evolve in parallel with early *Miogypsina* s.s., but the evolution of *L. thecidaeformis* via *L. droogeri* to *L. excentrica* takes place entirely within the range of *Miogypsina globulina*. Further, the early *Miogypsinoides* species show a reversal of the normal trend to nepionic reduction in that *M. complanata* has a larger spiral than *M.* cf. *bermudezi* ('nepionic retardation'). *Miogypsina globulina* is taken as an example of 'arrested evolution'. These results provide clear evidence of different rates of evolution in different lines and show that the application of the miogypsinoids in biostratigraphy is subject to the same constraints as that of *Cycloclypeus*. Nevertheless, the range zones, cross-checked by the planktonic foram zones, provide good correlation with the European stages.

PALAEOGEOGRAPHICAL PROVINCES

Although the large rotaliids represent a restricted facies and evidence of their former range is necessarily incomplete, it is clear (Vaughan, 1933; Dilley, 1971, 1973; Gorsel, 1978) that the late Cretaceous orbitoids occupied a worldwide, low latitude belt (figure 13.7). They were particularly abundant in the Caribbean area and western Tethys but also ranged through the Indonesian area and the Pacific. Some genera, such as *Omphalocyclus, Orbitoides* and *Schlumbergeria* occur in all these areas but other genera show a more restricted distribution which allows two main provinces to be distinguished (Gorsel, 1978):

(1) A Caribbean/Tropical Pacific province characterised by abundance of *Sulcoperculina* and members of the Pseudorbitoididae.

(2) A Tethyan/Indo-Pacific province characterised by *Pseudosiderolites* and members of the Lepidorbitoididae, together with calcarinids and *Simporbites*.

As pointed out by Gorsel, modern work in classification and on distribution largely confirms Vaughan's original ideas on the provincial development of the Cretaceous orbitoids.

The map (figure 13.7) shows the rather curious geographical occurrence of these forams at the present day. This reflects the drift of the continents north since the Santonian (Dilley, 1973) and in particular the displacement of former western Tethys by the northward drive of Africa through some 10° of latitude. India formerly lay alongside Madagascar. This island remains well south of the equator as evidence that the orbitoids once extended to approximately palaeolatitude 45° in both hemispheres (see maps in Smith and Briden, 1977).

With the return of the large rotaliids after the end-Maastrichtian extinctions, these two major provinces were again established but with a strong tendency for the development of subprovinces in western Tethys and the Indo-Pacific. These differences became sharp after the closure of western Tethys, the creation of the Mediterranean and its subsequent conversion in the late Miocene into a huge salt lake (Adams, 1967, 1973, 1976).

During the Palaeocene and Eocene the differences between the Caribbean province and the Tethyan/Indo-Pacific province were considerable. Both the Discocyclinidae and Lepidocyclinidae originated in America and although the discocyclines rapidly attained worldwide distribution most of the species in the Caribbean are different. They also die out at the end of the Middle Eocene while continuing elsewhere through the Upper Eocene. The lepidocyclines appeared in the early Middle Eocene and are practically confined to America until the Oligocene (apart from certain elements which reached the West African shelf and some doubtful, rare European occurrences). The Tethyan/Indo-Pacific region was distinguished by the abundance of *Nummulites* and *Assilina,* together with *Discocyclina* and *Spiroclypeus.* The nummulites apparently arose in western Tethys and rapidly spread to the Indo-Pacific but only a few migrated westwards to America. The very large Middle Eocene species (like the very large alveolines) did not reach the Indo-Pacific either, there being only one such species, *N. javanus,* which is endemic. The assilines did not reach America, although cordate operculines close to *Ranikothalia* are abundant and may have arisen here. Large rotaliids reached their widest latitudinal distribution during the Middle Eocene, especially *Asterocyclina* which reached palaeolatitude 45° in the North Atlantic (Porcupine Bank) and in the South Pacific (South Island, New Zealand) and even Alaska in the N. Pacific (? palaeolatitude 65°, see maps in Smith and Briden, 1977). This coincides with the acme of Tertiary marine transgressions and related climatic optimum.

Upper Eocene species are smaller than those of the Middle Eocene and a considerable reduction of diversity took place in the Lower Oligocene. The Tethyan/Indo-Pacific province is distinguished by small, radiate to sigmoid and reticulate nummulites, none of which reached the Caribbean province. However, *Nephrolepidina* reached western Tethys in the reverse direction and the Indo-Pacific subprovince was distinguished by the appearance of *Cycloclypeus.*

During the Middle Oligocene, *Eulepidina* and *Nephrolepidina* which appeared in the Far East together, became universally distributed in low latitudes. The largest reticular nummulite, *N. fichteli/intermedius* was widespread in Tethys and died out at the end of this stage. *Cycloclypeus* now appeared in western Tethys (Spain) also but possibly represented a separate evolutionary lineage from *Heterostegina* (MacGillavry, 1962).

During the Upper Oligocene and early Lower Miocene, after the extinction of *Nummulites* s.s., the large rotaliid faunas show least provincial development and *Spiroclypeus, Eulepidina* and *Nephrolepidina* occur world wide, although there are differences at species level. However, *Cycloclypeus* remained confined to Eurasia. *Miogypsinoides* appeared in the Upper Oligocene (possibly even in the Middle Oligocene in America) and gave rise to *Miogypsina* near the Neogene boundary. The distribution of this main stock of miogypsinids was also world wide and *Miogypsina,* like *Nephrolepidina,* reached as far south as New Zealand, palaeolatitude 40°S.

By the late Lower Miocene, the closure of Tethys with the creation of the Mediterranean and the appearance of new genera of alveolines in the Indo-Pacific led to a sharpening of differences between the provinces which became marked in the Middle Miocene. *Cycloclypeus* and the lepidocyclines now became confined to the Indo-Pacific. In addition, although *Miogypsina* persisted into the Middle Miocene in America and in the Mediterranean, the *Lepidosemicyclina* lineage and late species of *Miogypsinoides* are restricted to the Indo-Pacific.

The development of the Indo-Pacific as a separate province continued through the late Cenozoic after the final extinction of the annular and subannular complex rotaliids towards the end of the Middle Miocene. *Cycloclypeus* has ranged down to the Recent and there was a considerable proliferation of reefal calcarinids, including the appearance of *Baculogypsina,* in the Pliocene.

Of particular interest in the history of development of these provinces is the importance of the 'Tethyan Corridor' for the dominantly (although not exclusively) west to east migration of species, underlined by the sharp differentiation of the Indo-Pacific province after its disruption. The Atlantic acted as a partial barrier and the east Pacific as a more considerable one. As pointed out by Adams, migration was most rapid during the Palaeocene and in the early Oligocene, probably indicating the possibilities opened up for adaptive radiation following times marked by extinctions and reduced diversity. It is intriguing to note that the discocyclines disappeared in the Caribbean with the advent of the Lepidocyclinidae and that the lepidocyclines only spread eastwards into Eurasia in numbers after the nummulites had passed their acme, which may indicate competition for broadly the same environmental niche. Although Adams (1967) emphasised, with true scientific caution, that the results of the study of these larger rotaliids cannot be expected to hold good for other groups of organisms, unless they are adapted to the same range of environments and similarly limited by lack of a planktonic larval stage (?), the importance of these results for palaeogeography is manifest.

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SUMMARY CLASSIFICATION

MAIN FAMILIES AND IMPORTANT GENERA OF ROTALIIDS (LARGER)

ROTALIIDA	wall calcitic, hyaline perforate, radial, oblique or compound, bilamellar and may develop septal flap and canal system; planispiral or trochospiral to spreading or aborescent, annular discoid or annular complex; aperture characteristically ventral umbilical or basal and may extend over periphery on to dorsal side, multiple in advanced forms; Trias. – Rec. Key figures 13.8, 13.9 and 13.10.
ROTALIACEA	septal flap, septal fissures or subsutural septal canals, spiral septal canals and umbilical canals; dense radial canals through outer lamellae in some genera; trochospiral to planispiral, annular conical or annular complex; U. Cret. – Rec.
ROTALIIDAE	trochospiral with septal fissures and umbilical plug or numerous pillars; aperture ventral basal to multiple; U. Cret. – Rec. Key figure 13.8.
Rotalia (nos. 1 – 3)	small, up to 3 or 4 whorls, with ventral umbilical boss; marked septal fissures extending to divide boss into numerous pillars, pillars not continuous from one whorl to the next, aperture ventral basal with umbilical extension to umbilical canal; U. Cret. – Rec. (rounded periphery, pronounced umbilical lobe but no spiral canal and pillars extending to proloculus = *Ammonia* (nos. 4/5), Neo. – Rec.; single plug, carinate, with chambers lobate or produced into spines = *Pararotalia* (no. 9).
Lockhartia (nos. 6 – 8)	large, up to 5 mm dia., subconical; dorsal surface ornamented with nodes or ridges; umbilicus filled by vertical pillars with intercommunicating sub-labyrinthic cavities between; chambers communicate via cavities through pores between pillars on umbilical surface; Palaeocene – M. Eoc. (elongate = *Sakesaria,* Pal. – L. Eoc.; strong vertical canals = *Kathina,* U. Cret. – Pal.; intercalated whorls also = *Dictyokathina,* Pal.; intercalated whorls and horizontal plates between pillars = *Dictyoconoides* (no. 10), M. Eoc.).
CHAPMANINIDAE	conical, trochospiral to annular; tubular apertural system; M. Eoc. – Mio. Key figure 13.8.
Chapmanina (nos. 11/12)	annular conical with peripheral secondary septa, fissured at umbilical surface; multiple apertures with internal tubes to previous septum; M. Eoc. – M. Mio. (elongate, costate and lacking secondary septa = *Ferayina* (no. 13), M. Eoc.).
MISCELLANEIDAE	asymmetric to planispiral, involute; marked fissures or dense radial canals; aperture basal median to multiple; U. Cret. – Eoc. Key figure 13.8.
Fissoelphidium (nos. 24/25)	globose; dendritic fissures along sutures and finely divided umbilical boss, basal multiple apertures; U. Cret. (angular lenticular; reticulate ornament with chevrons over fissured sutures = *Cuvillierina,* Eoc.).

Miscellanea (nos. 21 – 23)	angular lenticular with few whorls and high chambers; test surface completely divided into bosses and nodes with large pillars in umbilical area; Palaeocene (flattened = *Daviesina*).
Pseudosiderolites (nos. 26/27)	angular lenticular with few whorls and chambers and numerous radial canals; umbilicus filled with pillars; U. Cret. (incipient lateral chamberlets = *Arnaudiella;* double layer of chambers with thick lateral laminae = *Biplanispira,* Eoc.).
CALCARINIDAE	trochospiral to planispiral, thickened lamellae with radial canals, spines in plane of coiling, becoming globular with chamberlets; U. Cret. – Rec. Key figure 13.8.
Calcarina (nos. 14/15)	trochospiral, biconvex with peripheral spines; aperture ventral basal; U. Cret. – Rec. (planispiral = *Siderolites,* U. Cret. – L. Eoc.).
Baculogypsina (nos. 16)	globular with radial tiers of chamberlets; spines arising from juvenarium; Mio. – Rec. (trigonal with 3 or 4 thick spines = *Baculogypsinoides,* Eoc. – Rec.).
MIOGYPSINIDAE	subannular complex, with partial rings of arcuate to ogival equatorial chambers developed on only part of the circumference, test angle typically less than 150°, with eccentric embryon giving a fan shape; thick lateral lamellae or tiers of lateral chamberlets with pillars; U. Olig. – M. Mio. Key figure 13.8.
Miogypsinoides (nos. 17/18)	prominent spiral juvenarium in both generations, may make up a large part of test; no lateral chamberlets; U. Olig. – L. Mio.
Miogypsina (nos. 19/20)	juvenarium close to periphery; spiral nepion reduced and embryon usually bilocular, in meg. gen.; lateral chamberlets well developed but usually rather irregular; L. – M. Mio. (juvenarium subcentral = *Miolepidocyclina;* hexagonal chamberlets = *Lepidosemicyclina*).
LEPIDORBITOIDIDAE	annular complex; small bilocular embryon in meg. gen. in which deuteroconch embraces the protoconch, nepion a long, primary spiral in early forms, 1 or 2 auxiliary and adauxiliary chambers in advanced forms; equatorial chambers spiral to annular, arcuate to hexagonal (spatulate); stolons diagonal, annular also between hexagonal chambers; U. Cret. Key figure 13.9.
Helicorbitoides MacGillavry 1963 (nos. 1/2)	nepion a single (uniserial) long primary spiral; spiral retained in equatorial layer after introduction of retrovert apertures and annular growth reached only at periphery; Camp.
Lepidorbitoides (nos. 3/4)	nepion a reduced, single, primary spiral and/or a double series, or a quadruple series; annular growth comes in earlier in advanced forms, primary spiral lost entirely in forms with quadruple nepion and adauxiliary chambers appear in the most advanced forms; Camp. – Maas. (small with relatively large juvenarium and sulcate nepion, annular throughout

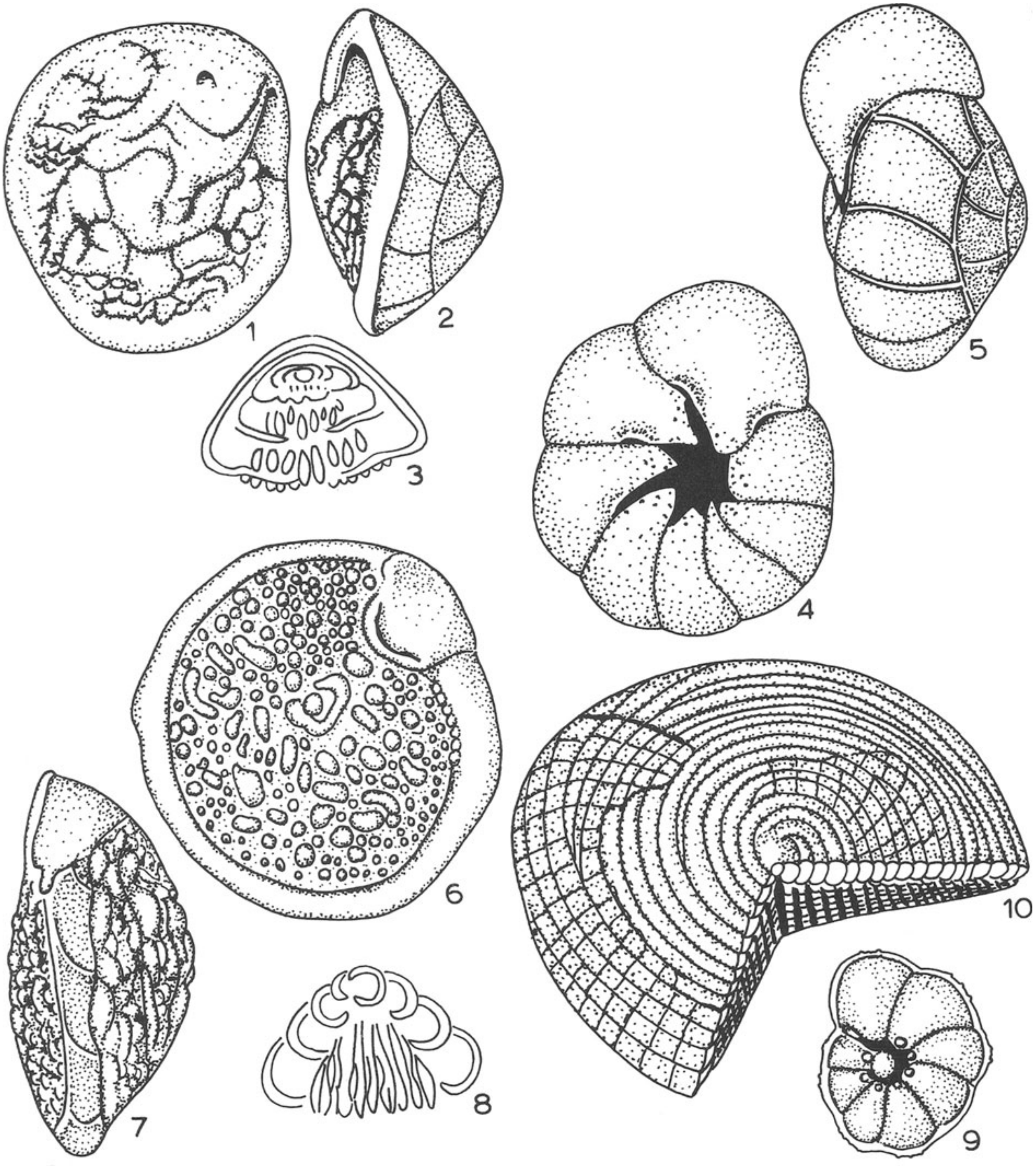
	equatorial layer = *Orbitocyclina*; rays in equatorial layer also = *Asterorbis*).
NUMMULITACEA	planispiral with septal flap and subsutural septal canals (with branches to sutural openings), marginal cord and marginal spiral canal system; advanced forms subannular to annular discoid and complex with cord modified or lost and marginal canals replaced by secondary intraseptal canals; U. Cret. – Rec. Key figures 13.9 and 13.10.
NUMMULITIDAE	planispiral with septal canals and spiral canals ramifying in marginal cord; umbilicus canaliculate, closed with boss or pillars which may also occur along septal and spiral sutures; single foramen, areal stolons and passages to canals in roof and to umbilicus formed by resorption; Palaeoc. – Rec. Key figure 13.9.
Sulcoperculina (nos. 5/6)	asymmetric involute; marginal cord with median sulcus and spiral canal, radial plates projecting into interior; U. Cret.
Nummulites (nos. 7/8)	involute, lenticular to subglobular; tightly coiled with numerous whorls and chambers, septa radial, sigmoid, meandrine or reticulate; septal canals ramify and may interconnect radially; Palaeoc. – Olig. (loosely coiled with few whorls = *Operculinoides,* Eoc. – Mio.).
Operculina (nos. 9/10)	involute to evolute, lenticular to compressed; loosely coiled with few whorls and high chambers; septal canals forked or ramifying; Palaeoc. – Rec. (enlarged marginal cord with coarse canal system, simple vertical septal canals = *Ranikothalia,* U. Pal. – L. Eoc.; tightly coiled = *Assilina* (nos. 11/12), Palaeoc. – Eoc.; flange of flat, semi-circular evolute chambers = *Operculinella,* Mio. – Rec.).
CYCLOCLYPEIDAE	subannular discoid to complex with lateral chamberlets and annular discoid; equatorial chamberlets rectangular to hexagonal; apertures multiple, peripheral, stolons Y-shaped or L-shaped to crossed over diagonal in advanced forms; Eoc. – Rec. Key figure 13.9.
Heterostegina (nos. 13/14)	evolute, subannular discoid with loosely planispiral arcuate chambers divided into chamberlets which alternate from chamber to chamber; Eoc. – Rec. (meg. gen. with annular chambers in adult = *Cycloclypeus,* Olig. – Rec. (nos. 15/16); marked rays also = *Radiocycloclypeus,* Mio.; raised rings = *Katacycloclypeus,* Mio.).
Spiroclypeus (nos. 17/18)	subannular complex with equatorial layer of loosely planispiral, arcuate chambers divided into alternating chamberlets and tiers of lateral chamberlets on either side; U. Eoc. – L. Mio.
PSEUDORBITOIDIDAE	annular complex in advanced forms with ring-like equatorial chambers crossed by vertical, radial plates (rods); earlier forms without equatorial chambers (questionable arcuate chambers in some species) with lateral chamberlets resting directly upon plates which may form peripheral flange; U. Cret. Key figure 13.10.

Pseudorbitoides (nos. 1/2)	lateral chamberlets resting directly upon plates in early species, ? arcuate equatorial chambers in advanced species; Camp. – Maas. (long nepion and 2 alternating systems of plates = *Sulcorbitoides,* Camp.; more than 2 sets = *Rhabdorbitoides,* U. Camp. – Maas.).
Vaughanina (no. 3)	nepion short, followed by annular chambers and 2 alternating systems of plates separated by a gap; U. Camp. – Maas.
DISCOCYCLINIDAE	annular complex, characteristically with fine equatorial layer and small, lateral chamberlets; juvenarium central, planispiral in micro. gen., bilocular with protoconch almost completely embraced by deuteroconch in meg. gen., equatorial chamberlets when present, formed by subdivision of ring-like chambers, rectangular to elongate hexagonal, connected by radial and annular stolons; Palaeoc. – Eoc. Key figure 13.10.
Pseudophragmina (no. 4)	single layer of equatorial chambers; chamberlets may be indistinct or absent, when present with distal annular stolons, tending to be in alignment in adjacent annuli; Palaeoc. – U. Eoc. (stellate = *Asterophragmina,* U. Eoc.).
Discocyclina (nos. 6 – 8)	single layer of equatorial chambers with well-developed chamberlets, usually alternating in adjacent annuli but may be in alignment; annular stolons mostly at proximal side; M. Palaeoc. – U. Eoc. (circular to stellate with equatorial layer multiplied in rays = *Asterocyclina* (no. 5) restricted to M. and U. Eoc. outside Western Asia and M. East, U. Eoc. in Oceania.).

ORBITOIDS WITHOUT CANAL SYSTEM

ORBITOIDIDAE (ORBITOIDACEA)	annular discoid to complex, biconcave to spherical; in early forms juvenarium of meg. gen. variable, embryon bilocular, nepion of 1 or 2 auxiliary chambers or a combination of spiral and alternating arrangements; in advanced forms embryon quadrilocular with thick integument, or reduced to 3 or 2 chambers; equatorial chambers arcuate to short hexagonal (spatulate); U. Cret. Key figure 13.10.
Orbitoides (nos. 9/10)	well-developed lateral chamberlets; juvenarium in meg. gen. consisting of quadrilocular embryon within integument, or reduced to 3 or 2 chambers, nepion of 4 – 20 epi-auxiliary chambers; Camp. – Maas. (lateral chamberlets absent or represented by a few low vacuoles, juvenarium in meg. gen. consisting of bilocular embryon and nepion which is spiral, alternating or of 1 or 2 auxiliary chambers only = *Schlumbergeria,* Sant. – Camp.; very large multilocular embryon = *Simporbites,* U. Maas.).
Omphalocyclus (nos. 11/12)	annular discoid, biconcave with equatorial layer of arcuate chambers ('engine turned appearance') doubled and trebled towards periphery; juvenarium

	in meg. gen. with quadrilocular embryon and nepion of 4 epi-auxiliary chambers; Maas. (spherical with no median layer and chambers in radial rows = *Torreina).*
LEPIDOCYCLINIDAE (ASTERIGERINACEA)	involute trochoid with subannular rings of ventral secondary chambers to annular complex; primary spiral persisting into the equatorial layer or with annular rings of chambers following the nepion immediately; juvenarium in meg. gen. with bilocular embryon, the deuteroconch embracing in advanced forms; M. Eoc. – M. Mio. Key figure 13.10.
Helicostegina (nos. 13/14)	involute trochoid with partial rings of secondary chambers on ventral side which may form peripheral band; M. Eoc. (annular complex with primary spiral persisting for up to 2 volutions with thick spiral band; rings of arcuate equatorial chambers incomplete until periphery = *Helicolepidina,* U. Eoc.).
Lepidocyclina s.s. (no. 18)	subequal bilocular megalospheric embryon; equatorial layer of annular rings of arcuate to hexagonal (spatulate) chambers; Olig. – L. Mio. (deuteroconch smaller than protoconch or 1 large chamber with peripheral smaller chambers = sub. gen. *Pliolepidina* (no. 19), M. – U. Eoc.; followed by spiral nepion also sub. gen. *Polylepidina* (no. 15), M. Eoc.; deuteroconch half embracing protoconch = sub. gen. *Nephrolepidina* (nos. 17/20), U. Eoc. – U. Mio.; deuteroconch almost completely embracing = sub. gen. *Eulepidina* (no. 16), Olig. – M. Mio.). N.B. *Trybliolepidina* = *Nephrolepidina* see Eames *et al.* 1962a.



Key figure 13.8 **Rotaliida (Larger), Rotaliacea**

1–3 ***Rotalia trochidiformis*** **(Lamarck), ventral and peripheral views, after L. & T., × 30; 3 vertical section, diagrammatic**

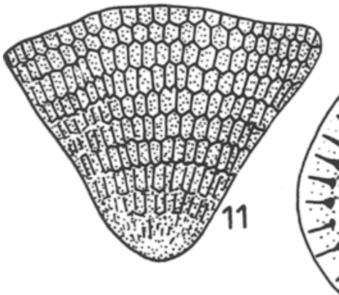
4/5 ***Ammonia aberdoveyensis*** **Haynes, ventral and peripheral views, × 100**

6–8 ***Lockhartia haimei*** **Davies, ventral and peripheral views, × 26; 8 vertical section, diagrammatic, after L. & T.**

9 ***Pararotalia inermis*** **(Terquem), ventral view, after L. & T., × 128**

10 ***Dictyoconoides cooki*** **(Carter); diagrammatic view of cutaway specimen, × 10 (approx.)**

Key figure 13.8 ***(continued)***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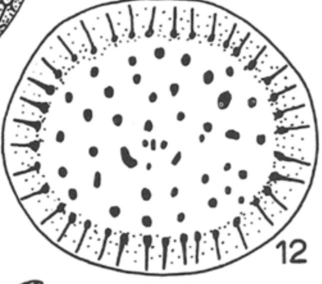
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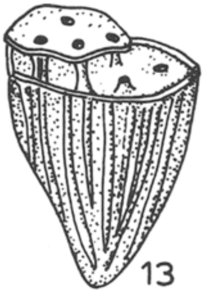
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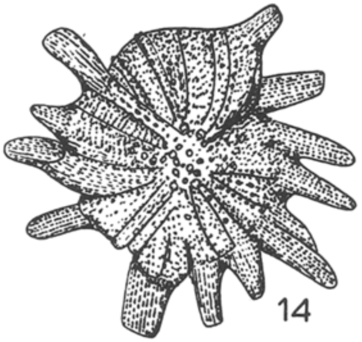
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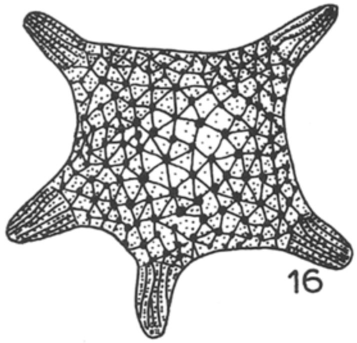
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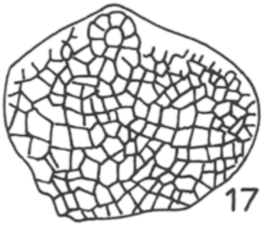
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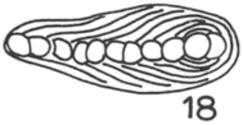
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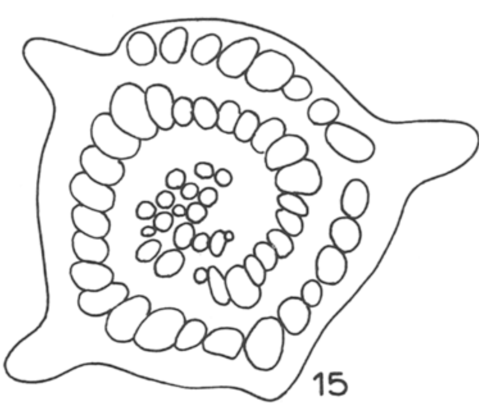
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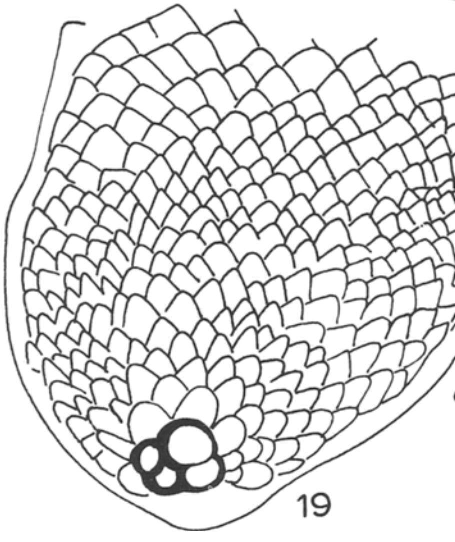
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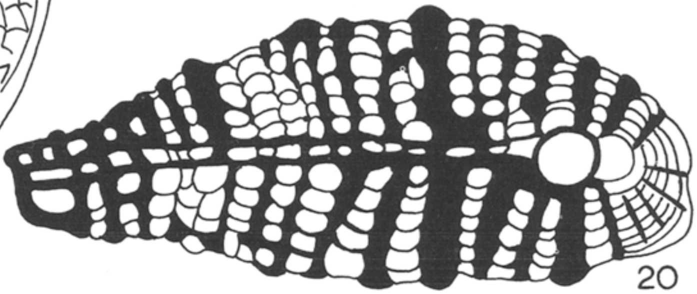
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11/12 ***Chapmanina gassineneis*** **(Silvestri), side and apertural views, after L. & T., × 35**

13 ***Ferayina coralliformis*** **Frizzell, breached specimen, after L. & T., × 105**

14/15 ***Calcarina spengleri*** **Gmelin, ventral view, after Brady, × 30; horizontal section, after Todd & Post, × 20**

16 ***Baculogypsina sphaerulata*** **(Parker & Jones), side view, after L. & T., × 20**

17 ***Miogypsinoides bantamensis*** **Tan, equatorial section, after Hanzawa, × 15**

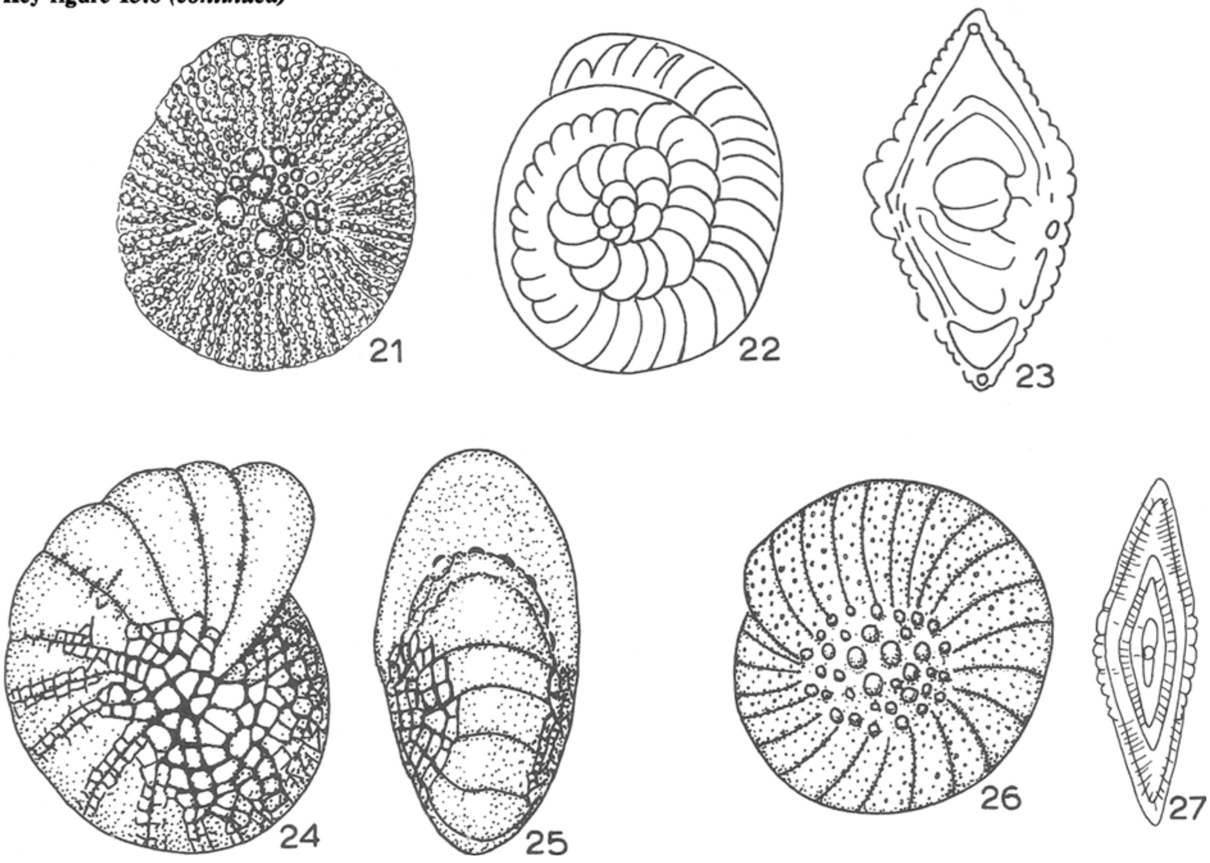
18 ***Miogypsinoides lateralis*** **Hanzawa; vertical section, × 15**

19 ***Miogypsina antillea*** **Cushman, equatorial section, after Cole, × 40**

20 ***Miogypsina cushmani*** **Vaughan, vertical section, after Cole, × 40**

(continued overleaf)

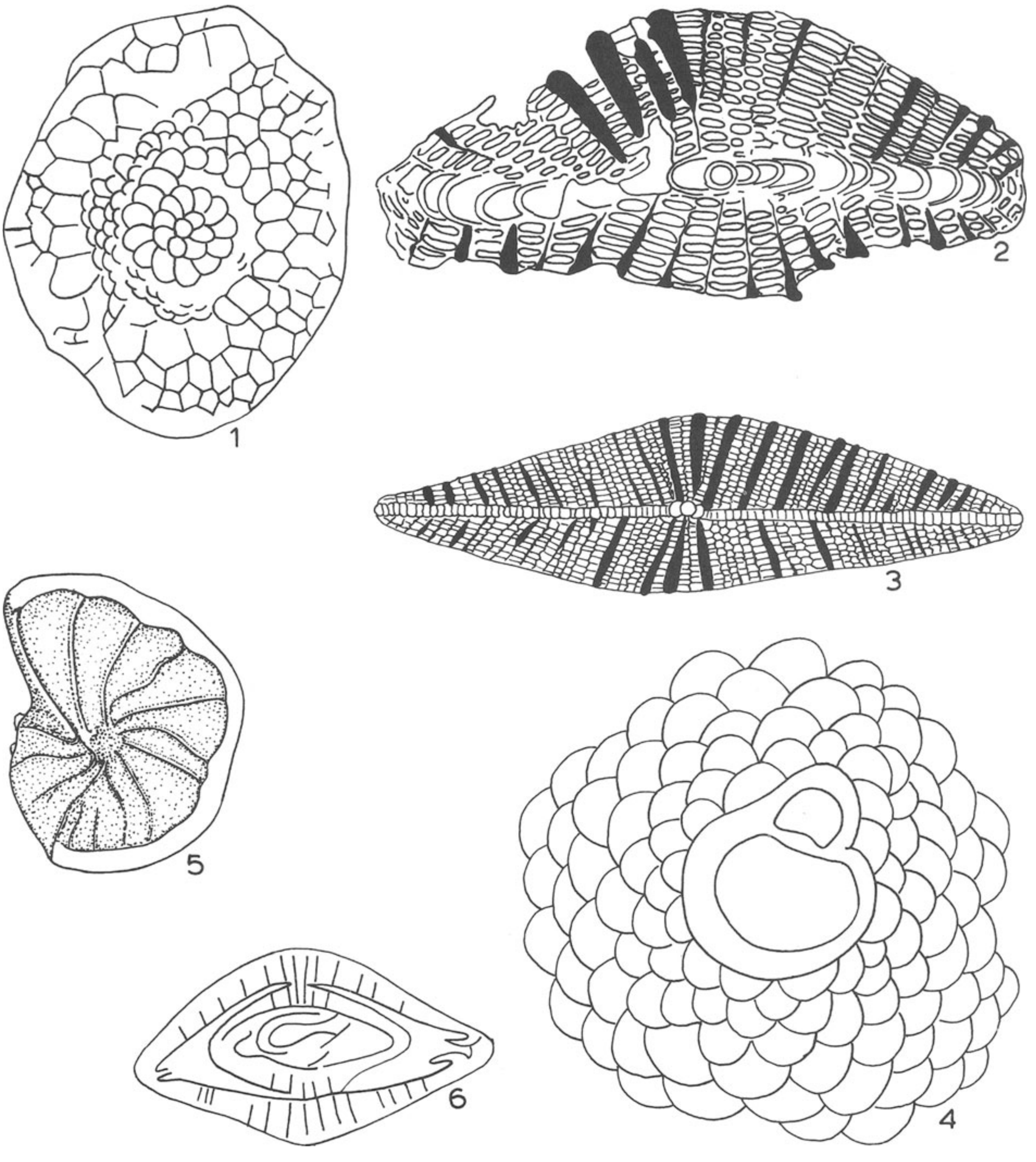
Key figure 13.8 ***(continued)***



21 – 23 *Miscellanea miscella* (Archiac & Haime), side view and horizontal and vertical sections, after L. & T., × 20

24/25 *Fissoelphidium operculiferum* Smout, side and peripheral views, after L. & T., × 28

26/27 *Pseudosiderolites vidali* (Douvillé), side view and vertical section, × 8



Key figure 13.9 Rotaliida (Larger), Rotaliacea, Nummulitacea

1/2 ***Helicorbitoides longispiralis*** **(Papp & Küpper), equatorial section, × 50; vertical section, × 35, after Gorsel**

3/4 ***Lepidorbitoides socialis*** **(Schlumberger), vertical section, after Tan, diagrammatic, × 10; equatorial section, × 128**

5 ***Sulcoperculina dickersoni*** **Palmer, side view, × 40**

6 ***Sulcoperculina cosdeni*** **(Applin & Jordan), vertical section, after Cole, × 38**

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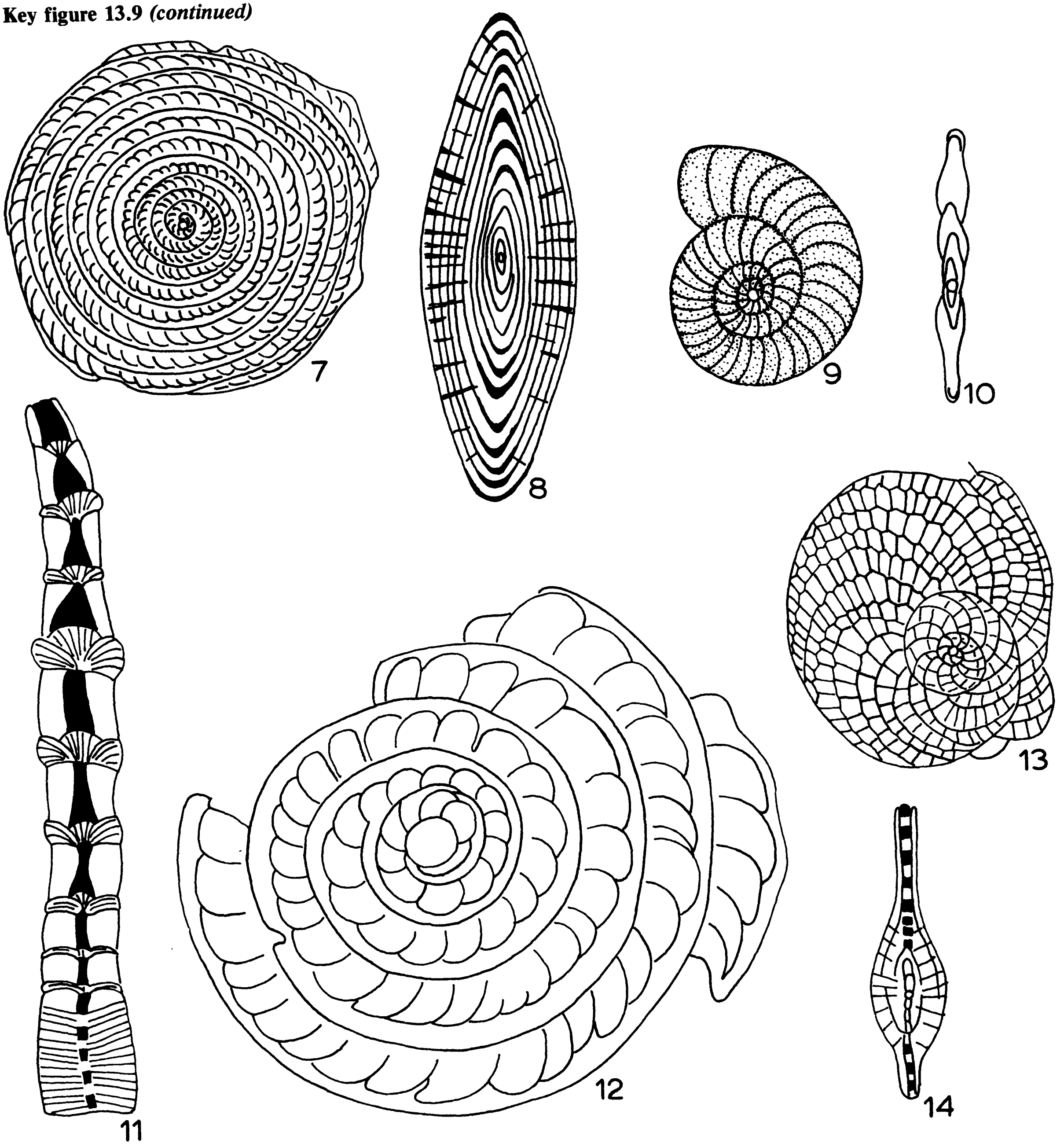
Key figure 13.9 *(continued)*



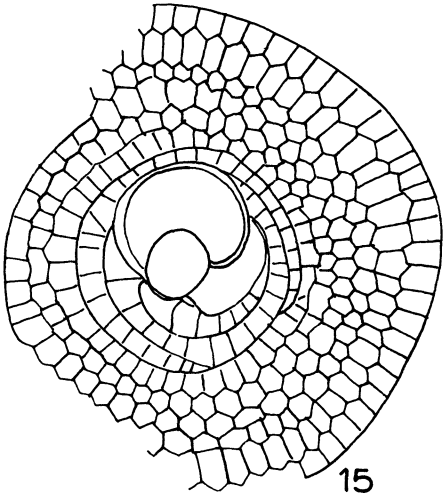
7/8 *Nummulites laevigatus* (Brugière), horizontal section, after Hantken, × 4; vertical section, after Favre, × 5

9/10 *Operculina ammonoides* Gronovius, side view and vertical section, after Hanzawa, × 10

11/12 *Assilina spira* (de Roissey), part vertical section, after Fortis, × 7; horizontal section, after Schaub, × 12.5

13/14 *Heterostegina depressa* (d'Orbigny), horizontal and vertical sections, after Tan, × 15

Key figure 13.9 ***(continued)***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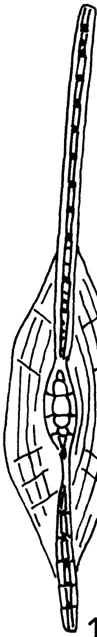
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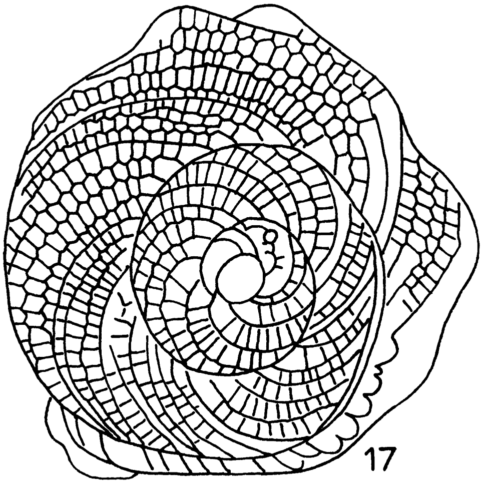
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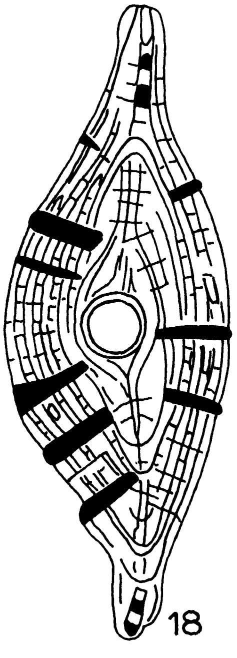
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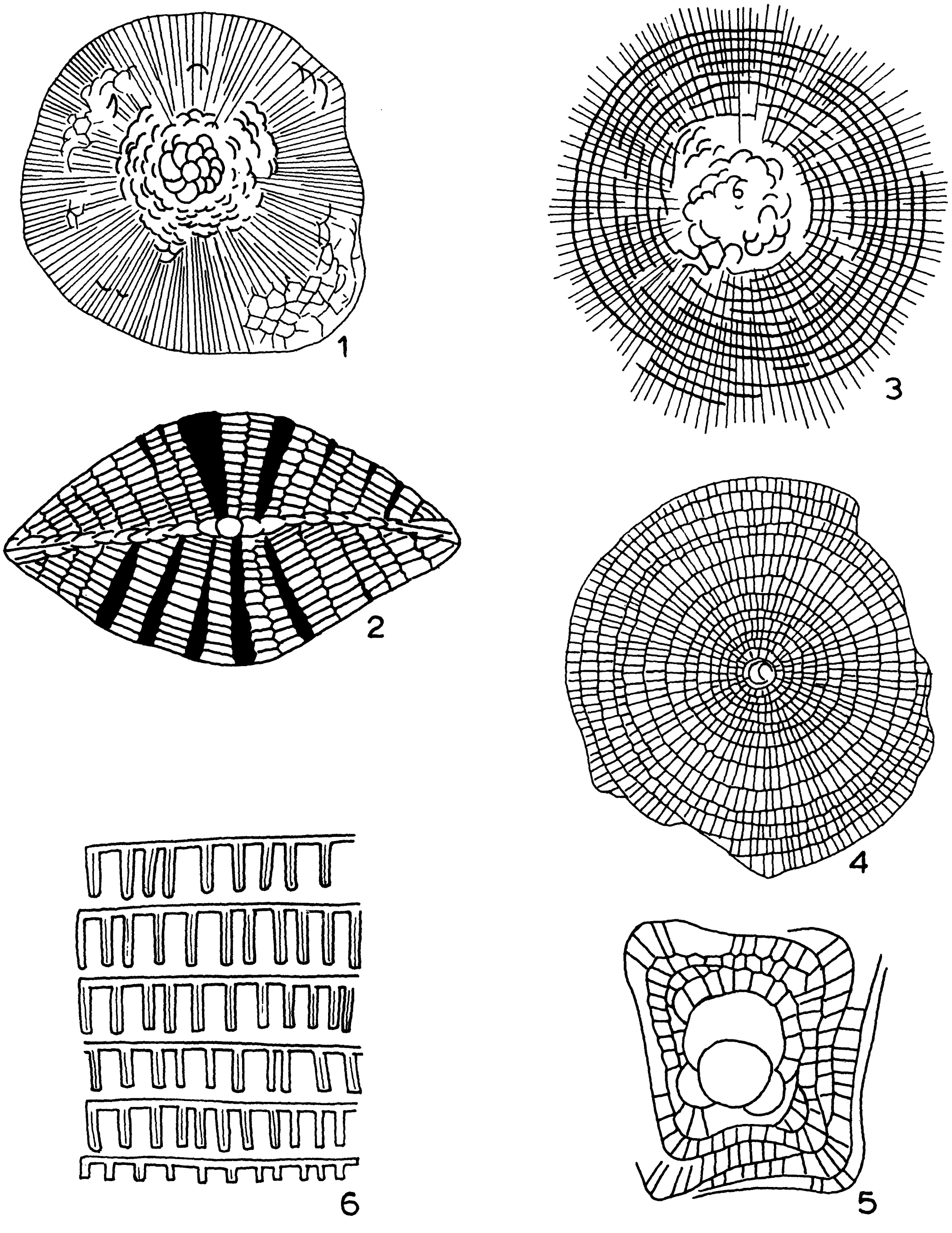
15/16 ***Cycloclypeus carpenteri*** **Brady, horizontal section, × 32; vertical section, × 16, after Cole**

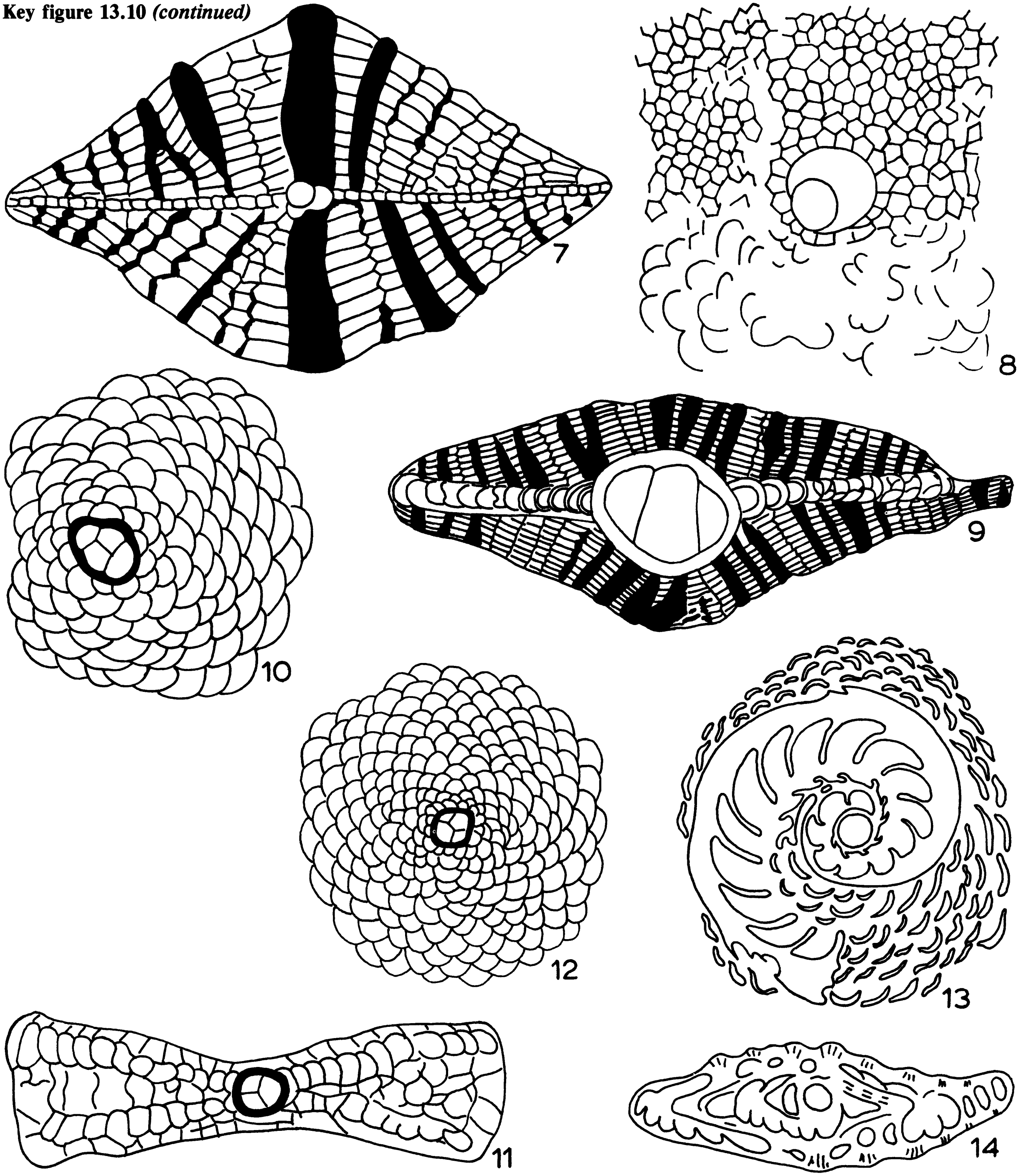
17/18 ***Spiroclypeus tidoenganensis*** **Vlerk, equatorial and vertical sections, after Cole, × 16**



Key figure 13.10 Rotaliida (Larger), Nummulitacea, Orbitoidacea, Asterigerinacea

- **1/2** ***Pseudorbitoides israelskyi*** **Vaughan & Cole, equatorial section, × 30; vertical section, × 40**
- **3** ***Vaughanina cubensis*** **Palmer, equatorial section, × 38**
- **4** ***Pseudophragmina flintensis*** **(Cushman), equatorial section, after Cole, × 40**
- **5** ***Asterocyclina asterisca*** **(Guppy), equatorial section of embryon and first few equatorial chambers, after Brönnimann, × 85**
- **6** ***Discocyclina pratti*** **(Michelin), equatorial section showing portion of equatorial chambers with canals, after Vaughan, × 85**

Key figure 13.10 *(continued)*



7/8 *Discocyclina douvillei* (Schlumberger), vertical section, × 43; equatorial section, × 52, after Neumann
9 *Orbitoides apiculata* Schlumberger, vertical section, after Silvestri, × 22
10 *Orbitoides media* (Archiac), equatorial section, after Cole, × 40
11/12 *Omphalocyclus macroporus* (Lamarck), vertical section, after Cole, × 20; equatorial section, after Schifsma, × 13
13/14 *Helicostegina dimorpha* Barker & Grimsdale, horizontal and vertical sections, × 43

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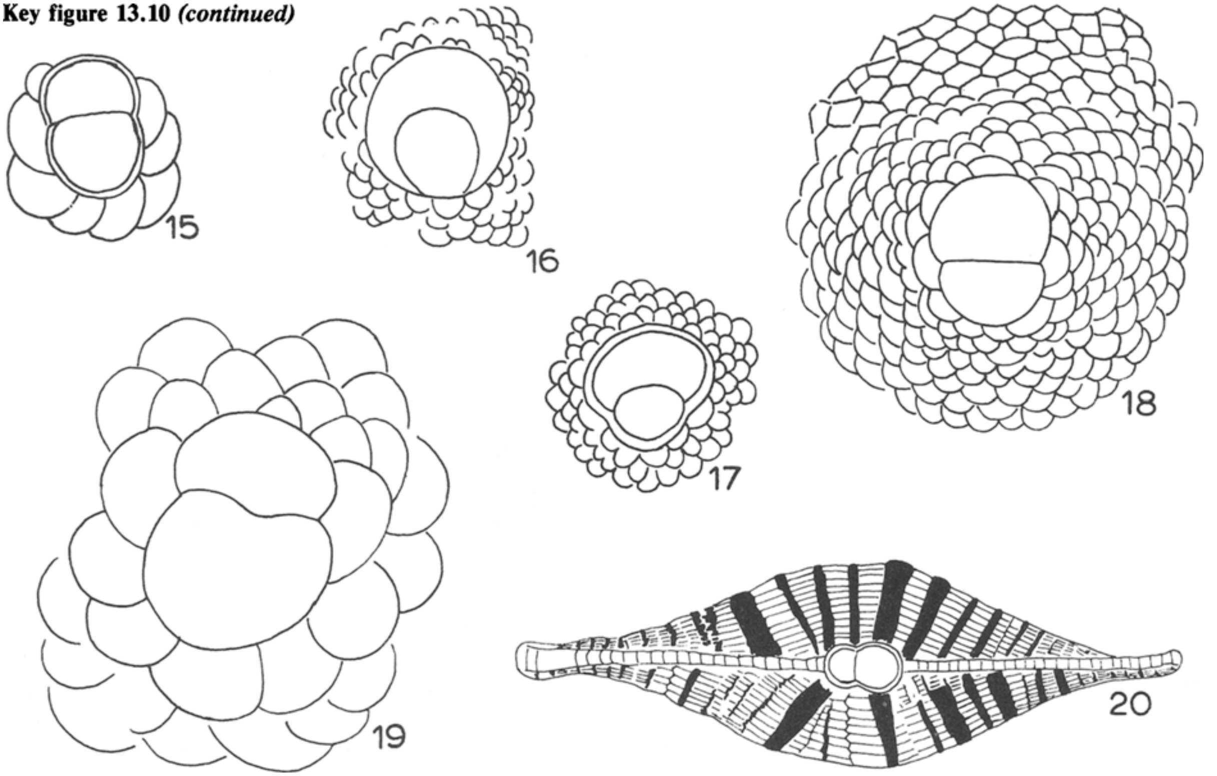
Key figure 13.10 *(continued)*



15 ***Lepidocyclina (Polylepidina) antillea*** **Cushman, equatorial section of embryon, after Cole, × 65**

16 ***Lepidocyclina (Eulepidina) formosa*** **Schlumberger, equatorial section of embryon, after Cole, × 40**

17 ***Lepidocyclina (Nephrolepidina) tournoueri*** **Lemoine & Douvillé, equatorial section of embryon, after Cole, × 40**

18 ***Lepidocyclina (Lepidocyclina) mantelli*** **Martin, after Cole, × 40**

19 ***Lepidocyclina (Pliolepidina) proteiformis*** **Vaughan, equatorial section of embryon, × 80**

20 ***Lepidocyclina (Nephrolepidina) verbeeki*** **Newton & Holland, vertical section, after Cole, × 20**

Chapter 14

The Globigerinida

Unmarked and trackless though it may seem to us, the surface of the ocean is divided into definite zones, and the pattern of the surface water controls the distribution of its life.

(Rachel Carson, 1951)*

Members of the Globigerinida constitute up to 10 per cent of the zooplankton in the oceans and may exceed 60 per cent in certain areas in summer (King and Desmond, 1953). Although they accumulate very slowly their microscopic, dead shells have laid down a blanket of 'Globigerina Ooze' on the deep ocean floor. This ooze is usually masked by terrigenous sediment on the shelves but it occurs, often in remarkably pure form, on the Abyssal Plain. It is the dominant sea floor deposit from approximately 600 m down to the Calcite Compensation Depth at about 4500 m, where it is gradually replaced by Siliceous Ooze and Red Clay. As noted earlier, it covers almost half of the total, deep ocean floor and is therefore the most extensive organic sediment on earth.

The globigerine 'snowfall' has continued since the late Jurassic and spans almost the entire history of development of the modern oceans, producing vertical sequences of up to 1 km thickness near the margins. The great value of planktonic Foraminifera in stratigraphy which rests on their wide distribution and rapid evolution was pointed out in chapter 1. Their particular value in the analysis of the sequences of deep sea deposits which have become available since the beginning of the Deep Sea Drilling Project (JOIDES and IPOD) has been well expressed by Berggren (1978). He points out that micropalaeontology plays a central role in providing a geochronological framework within which the evolution of the oceans can be studied and that: 'Late in 1968, in the course of drilling the South Atlantic, micropaleontology had one of its finest moments as the estimated ages of planktonic (foraminiferal) biozones helped to establish the fact that there was, as predicted by the sea-floor spreading model, an essentially linear relationship between basement age and distance from a spreading axis.

The wide distribution and rapid evolution shown by planktonic Foraminifera are a reflection of their successful colonisation of the pelagic realm. This warrants some discussion of the adaptive features which have made possible such a radical departure from the paths followed by most other Foraminifera.

The Globigerinida are apparently unique among the Foraminifera in their ability to lead a fully planktonic life, which means they can maintain themselves in the surface or near-surface waters of the open ocean without sinking. This is a vital requirement for symbiotic species which must stay in the photic zone and for species which feed on other members of the plankton. Because living matter, as well as the test, is heavier than sea water, special physiological adaptations are required to give positive buoyancy together with modifications of the hard parts to help lower the sinking rate.

The means by which buoyancy is achieved are not fully understood but include the development of an extended, frothy ectoplasm with gas vacuoles and fatty or oily droplets, giving rise to a definite flotation bubble or capsule in *Hastigerina*. According to Hansen (1975) the function of the 'vesicular reticulum' in globigerinids, mentioned earlier, may be to substitute heavy ions for light ones, causing the animal to rise and sink diurnally. If this, or a similar process, does prevail then the importance of lowering the day-time sinking rate is critical. This may be assisted by increase in the amount of protoplasm relative to the test. In *Orbulina* this may come about by simple increase in size during ontogeny; the protoplasm tends to increase during growth proportionately to the cube of the diameter of the test, whereas the mass of the test increases proportionately to the square of its diameter and the juvenile chambers are resorbed. Larger, relatively lighter individuals may thus be favourably adapted to warmer (less viscous) waters of the tropical, near-surface (epipelagic) zone. This process will be effective up to the point where increasing size begins to markedly decrease the surface/volume ratio of the test, apparently up to 1 mm diameter (which explains why most planktonic organisms are microscopic and less than 1 mm in size).

**The Sea Around Us*. Staples Press, Norwich.

The sinking rate may also be lowered by economy in the use of shell material and it was noticed very early (Rhumbler, 1911) that near-surface specimens of *Orbulina* had thinner walls than specimens apparently living at greater depth. Lowering of the sinking rate is also brought about by modifications of the test that increase frictional drag. These include the development of long spines, up to three times the test diameter, as in *Globigerina* which also serve to help spread out and support the ectoplasm and pesudopodial network. When earlier spines penetrate through the chambers of later whorls, as in *Hastigerina,* they may also have an architectural strengthening function. Further modifications include flattening of the test in the horizontal plane, often with radial extension of the chambers which may become club-shaped or clavate. Such forms are usually smooth but may have spines at the periphery or on the ends of the chambers (*Hastigerinopsis*).

The common occurrence of keels in the flattened genera has been explained as a simple response to the bending stresses at the periphery (Scott, 1973a, 1973b). As well as acting as a 'buttress', the keel may help to spread out the pseudopodial network in the horizontal plane, as noted earlier in *Amphistegina*.

The viscosity of sea water near freezing point at 0°C is twice that at 25°C and the problem of sinking rate is not so serious for subpolar species such as *Turborotalia pachyderma* which has relatively thick walls. It is also significant that a number of non-spinose globorotaliids, such as *G. truncatulinoides,* develop a thick 'calcite crust' at a late stage in their life cycle, which might enable them to keep station at lower depths (mesopelagic); this may amount to an increase of almost 50 per cent in total weight. It will therefore be seen that specialised modifications to increase frictional drag are the particular requirement of tropical and epipelagic temperate genera which have to cope with an accelerated sinking rate in warm water: this has important applications in palaeogeographical studies, see further below.

The increase in relative amounts of protoplasm and the differentiation of the ectoplasm has led to enlarged apertures and supplementary openings in this group. Globular forms tend to have multiple apertures and the attainment of a spherical test in *Orbulina* is linked with the possession of evenly distributed areal apertures to give efficient protoplasmic streaming in all directions. Relatively large pores probably also increase metabolic efficiency which can be expected to proceed at faster rates in warm water. It is interesting that Bé *et al.* (1976) and Bé (1977) find that both maximum diameter of the test and pore size in *Orbulina* increase towards the tropics and thus directly with water temperature.

CHAMBER FORM AND COILING MODES

Although incredibly abundant in individuals the Globigerinida are a relatively small order in number of genera. Fifty-nine (12 of them extant) were recognised in the 'Treatise', if *Cassigerinella* is excluded as a probable cassiduline. Some 150 names have now been suggested, although some are probably synonyms. As shown in figure 4.3, low trochospiral coiling is dominant (50 per cent) with 21 per cent planispiral. These figures are similar to those for the Rotaliida but the Globigerinida differ in the strong tendency towards inflated chambers and subspherical test shape, an additional 7 per cent becoming fully spherical or globular, with one genus unilocular and spherical. They also differ in the common development of laterally extended and clavate chambers and rugose, pitted and spinose surface textures as well as apertural coverplates.

The group also includes a high percentage (13 per cent) of biserial to uniserial and spreading genera (all extinct). This test form could be considered inappropriate in the planktonic realm and, in response, some workers have attempted to exclude *Bifarina* and its allies on the grounds of their supposed monolamellar wall structure. But the discovery that all the hyaline Foraminifera, apart from the Nodosariida, are bilamellar means that they cannot be so conveniently dismissed. Perhaps the high incidence of spreading growth is indicative of a quasi-planktonic habit attached to weed of Sargassum type.

The planktonic Foraminifera were originally included in the subfamily Globigerininae of Carpenter, Parker and Jones (1862), and recognised as a family by Brady (1884) to cover globigerine genera known from the modern, Globigerina Ooze. It was only realized later, from comparative morphology and distribution, that truncate and keeled forms from the Cretaceous were also planktonic. Both Cushman (1948) and Glaessner (1945, see reprint 1963a) grouped *Globorotalia* and *Globotruncana* together in the Globorotaliidae, but it has since become clear that the Mesozoic planktonics represent a number of separate families, most of which disappeared with the great, end-Maastrichtian extinctions.

The 'astounding volume' of new information which has accumulated on this group, especially concerning its stratigraphical relationships, over the past quarter-century, has led to considerable refinements in classification. Nevertheless, the problems caused by the strong tendency towards parallel development and convergence of different lines within the Globigerinida have not yet been overcome. There is still disagreement about the relative value of the different morphological characters in classification and despite the huge contribution of the Deep Sea Drilling Project much remains to be learned about stratigraphical range. For detailed historical accounts, see Loeblich *et al.* (1957) and El-Naggar (1971), together with Steineck and Fleisher (1978), for a discussion of the current attempt to include the ultrastructures revealed by SEM in evolutionary studies.

The chief differences between the classifications proposed are in the emphasis put upon aperture position as against the character of external apertural modifications and coiling mode, at family level. Thus Bolli, Loeblich and Tappan (1957) placed aperture position, coiling mode and apertural modifications in descending order of importance. On the other hand, Banner and Blow (1959) considered the external modifications of the aperture the most important, with shape and position only of subfamily significance. A different approach was taken by Lipps (1966) who attempted to distinguish the Cenozoic families on the basis of fine details of wall structure, including crystal size and whether the wall surface is smooth, pitted or spinose. He concluded that the 'obvious morphologic features' including aperture position and external modifications, are principally the result of convergence and not indicative of true relationships. However, most authors have continued to follow either Banner and Blow or the 'Treatise'. This is not only because the details of wall structure are still poorly known but because although certain families, such as the Globorotaliidae, are typically smooth, or are spinose, such as the Globigerinidae, there are many exceptions which cut across the groupings made on gross morphology. Also, not only do changes occur during ontogeny but many species develop 'crusts' of secondary calcite during life which makes these distinctions hard to apply.

There are similar differences between authors in the weight attached to various morphological details considered significant at lower taxonomic levels. Most workers accept modification of chamber shape and presence or absence of keels, or supplementary apertures, as generic, or (because gradational) as subgeneric. Some (Pessagno, 1967; Porthault, 1970; Longoria and Gamper, 1975) go further and regard the number of keels or the presence of a poreless peripheral band alone, as generic distinctions. There is less agreement about the value of particular apertural structures such as bullae, considered as of subfamily significance in the 'Treatise' but dismissed as infraspecific by Hofker (1959) and of not more than specific significance by El-Naggar (1971). Similar uncertainty surrounds the treatment of the details of surface texture and ornament. As a guide to current practice it can be said that in their treatment of Mesozoic planktonics, Longoria and Gamper (1975) are inclined to split while El-Naggar (1971) and Masters (1977) are inclined to lump. In regard to Cenozoic planktonics, Berggren (1977) is inclined to split, El-Naggar (1971) to lump, while Jenkins (1971a) and Stainforth *et al.* (1975) take a middle course.

The student should note that although stratigraphical occurrence may be a guide to evolutionary relationships, this kind of evidence is inconclusive unless species groups can also be discriminated by morphological criteria. As stressed in chapter 5, the temptation to take a particular feature as a 'key' to relationships should be avoided. He should also pay serious attention to the criticisms made by Stainforth *et al.* (1975) of the present state of the art in evolutionary studies as being subjective and lacking adequate documentation and statistical rigour. In these circumstances the use of fairly wide form genera has to be accepted as a matter of practical necessity (as in the case of the Nodosariida discussed in chapter 9). In this connection it is interesting that the results of an amino-acid assay indicate that the Recent planktonic species cluster according to generic distinctions made on gross morphology (King and Hare, 1972). The application of numerical methods to the study of the test of planktonic Foraminifera has been discussed by Scott (1966, 1967), Berger (1969a) and Malmgren (1974).

In the classification followed here (see the Summary Classification at the end of the chapter) the Cretaceous families, apart from the Guembelitriidae, are separated from the Cenozoic families and placed in two additional superfamilies, thus following Longoria and Gamper rather than Masters. These groups were originally separated because Banner and Blow believed that perforated apertural structures and coverplates did not appear until the Tertiary. This supposed difference between largely Mesozoic imperforate structures and Cenozoic perforate structures has since been found to be merely a matter of degree (Lipps, 1966), as is well shown in the excellent SEM photos of Longoria and Gamper (1975). Despite this discovery it seems clear that these structures represent parallel evolutionary developments in groups widely separated in time. The umbilical coverplates of the Mesozoic groups are developed by fusion of asymmetrical lips and flaps, whereas the covers of the Cenozoic globigerinids (bullae) appear to be formed by a process similar to chamber formation (they are therefore analogous, not homologous structures). The importance attached to these features by Banner and Blow is therefore accepted and, together with coiling mode and aperture position, is made the basis of the distinction of the four superfamilies.

Hedbergellacea

Low trochospiral genera with asymmetric lips or flaps which may be fused to form an umbilical coverplate are included in this superfamily. Three families are recognised: the Hedbergellidae covers those genera with simple flaps (portici) only (key figure 14.10); the Rotaliporidae covers those genera in which the flaps are partially fused to give a spiral 'platform' or coverplate (key figure 14.10) with marginal accessory apertures ('infralaminal'); and the Globotruncanidae covers those genera in which the flaps coalesce to give a fully developed tegillum (plate 14, no. 11) with both marginal and areal accessory apertures ('intralaminal').

Masters (1977) considers *Hedbergella* synonymous with *Globigerina* and has transferred *Praeglobotruncana* to the Rotaliporidae. This course is not followed here and the Hedbergellidae are considered to represent a distinct morphological group, separate from the Cenozoic Globigerinacea and characteristic of the Lower Cretaceous/Upper Cretaceous transition. Double-keeled forms of *Praeglobotruncana* have been distinguished as *Dicarinella* Porthault (1970). However, specimens of *P. delrioensis*, the type species for *Praeglobotruncana*, as illustrated by Michael (1972) appear to show a closely appressed double keel, so further study of this feature is required. Both smooth and rugose species of *Hedbergella* and *Praeglobotruncana* occur and species of *Hedbergella* such as *H. washitensis* with raised ornament of polygonal ridges have been distinguished generically as *Favusella* Michael (1972), although this feature is considered specific only by Masters (1977).

Formerly, it was supposed that there was a fundamental difference between the members of the Rotaliporidae with marginal accessory apertures, such as *Ticinella* and *Thalmaninella* and those which appeared to have secondary sutural apertures, such as *Rotalipora*. However, as shown by the good SEM photos of Eicher (1972) and discussed by Masters (1977) there is no essential difference between these three genera. The marginal accessory apertures appear sutural in the type species *R. cushmani*, largely as a function of chamber shape; *Thalmaninella* is therefore considered synonymous with *Rotalipora*.

The aperture in the Globotruncanidae is characteristically umbilical but becomes extra-umbilical in *Abathomphalus* which also has a tegillum formed by a single plate (techo). Both *Abathomphalus*, double keeled, and *Globotruncanella*, peripheral band only, are flattened, tabular forms with radiating ridges (costellae) near the peripheral margin. These have been taken as constituting family differences (Abathomphalidae Pessagno 1967) but, for the time being, are considered here of subfamily rank only. Many globotruncanids are rugose with raised sutures and umbilical shoulders and the *Rugoglobigerina* group developed characteristic 'meridional' nodes and costellae radiating from a point on the chamber.

Heterohelicacea

Trochospiral to planispiral and planispiral to biserial and spreading genera with median aperture bearing asymmetric flaps, lips or necklike extensions are included in this superfamily.

The Planomalinidae includes the trochospiral to planispiral genera with globular or compressed carinate chambers. On first sight the Schackoinidae, which includes genera with tubulo-spines or clavate chambers, appears to represent a logical development from within the Planomalinidae but as it appeared earlier in time it is separately distinguished.

Planispiral to biserial and diverging or spreading genera are included in the Heterohelicidae. Here the aperture becomes a high arch with a narrow lip and supplementary sutural apertures and chambers are commonly developed. Whereas planomalinids are mostly smooth the heterohelicids are generally ornamented with longitudinal costae.

Genera that are biserial throughout, with neck-like extensions to the aperture, are included in the Chiloguembelinidae.

Globigerinacea

This superfamily includes trochospiral to streptospiral genera with ventral umbilical to extra-umbilical aperture, characteristically bearing symmetrical lips (but sometimes developing umbilical teeth) with discrete umbilical coverplates (bullae) in advanced forms and multiple apertures (plate 15).

High trochoid genera with umbilical apertures and thick, simple lips are included in the Guembelitriidae. This family needs further study as it appears to have arisen in the Middle Jurassic. As discussed in chapter 11, the so-called Jurassic 'globigerinids' have been found to include both oberhauserellids and even reinholdellids (Robertinida). Masters (1977) recognises only two true Jurassic globigerinids. These should probably both be referred to *Caucasella* (type *'Globigerina' bathoniana* Pazdrowa 1969 = *'Globigerina' jurassica* acc. Masters)*.

Further problems beset the position of *Guembelitria.* According to Masters (1977), *G. cretacea,* the type species, has supplementary sutural apertures as well as distinctive perforated elevations, = 'pore mounds', on its surface. Masters regards Cenozoic occurrences as reworked but it is clear from the work of Jenkins (1974, 1978a, 1978b) on '*'Guembelitria' stavensis* (Eocene of Alabama) and *'G.' samwelli* (Oligocene, Australasia) that the Tertiary species are different in wall structure and lack pore mounds. Further work is required to show whether *'G' samwelli* which has supplementary apertures can be placed in *Guembelitrioides* El-Naggar (1971), as the type for that genus, *Globigerinoides higginsi* may not belong in this family. *'Guembelitria' stavensis* is made the type of a new genus, see below.

Cenozoic genera with low to moderate trochospire, globose chambers increasing rapidly in size as added, largely umbilical aperture and characteristically with symmetrical lips, umbilical teeth or bullae are included in the Globigerinidae. The bullate forms constitute a definite subgroup and further work may support the claim of Lipps (1966) that they warrant family status. One of the problems here is that these structures are not always developed during ontogeny.

The surface is typically spinose, although advanced forms may become smooth. The spines become detached on reproduction or death so that normally only the spine bases are retained. The 'hispid' appearance this imparts to the test wall is not always easily detectable and it is possible some apparently smooth species formerly did possess spines, attached to the external organic membrane. In many cases the pores are countersunk in pits, the edges of which may be raised to give a boxwork or reticulate ornament. The spines apparently then originate from the corners of the polygons or hexagons. Certain species, such as *Globigerina triloculinoides* in the Palaeogene, with prominent reticulation but presumed non-spinose, have been grouped in *'Subbotina'* and removed to the 'Catapsydracidae' by Lipps (1964, 1966). However, in practice it is not possible to distinguish between these species and spinose-reticulate species which have lost their spines. A further complication is that the well-grown lectotype of *Globigerina bulloides* has been shown by Yolande Lecalvez (1974) to be finely reticulate. The small specimens illustrated by Steineck and Fleisher (1978) and shown to be smooth are undoubtedly immature. Reticulation therefore varies with ontogeny in the type species of *Globigerina.* It is also well displayed in *Globigerinoides* and early forms of this genus in the Palaeogene have been distinguished as *Globoconusa* because they are high trochospiral and densely spinose. Again, both these features are well displayed in the Neogene type species of *Globigerinoides, G. ruber,* especially by its white form.

In *Pulleniatina* which becomes smooth in the adult the change is coincident with the change in coiling geometry to 'streptospiral' and overlapping (Burt and Scott, 1975). Although the displaced aperture becomes extra-umbilical in this genus, the morphology is otherwise globigerine. For this reason the genus is retained in the Globigerinidae, although it was removed to the Globorotaliidae by El-Naggar (1971). Similarly, the smooth *Candeina* is also retained within the Globigerinidae.

In a number of globigerinids the apertural lip is extended as a triangular umbilical tooth which remains visible as further chambers are added. These species have been placed in *Globoquadrina*

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*See, however, Grigelis and Gorbatchik (1980). *J. foramin. Res.,* 10(3):180–190.

in the past, but that genus appears to represent a stock within the Globorotaliidae, so a new name appears to be required for species such as *'Globoquadrina' larmeui* and *'G'. tripartita* which are non-quadrate.

The Globorotaliidae includes low trochoid genera which tend to develop an angular or carinate periphery and in which the aperture is largely or completely extra-umbilical. The surface texture is characteristically smooth to rugose (with growth of euhedral calcite rhombs—see Srinivasan and Kennett, 1974, 1976) but densely spinose forms, such as *Truncorotaloides,* occur in the Palaeogene.

Species showing morphology intermediate with *Globigerina* are difficult to classify. Thus *'Turborotalia' pseudobulloides* in the early Palaeogene has globigerine chamber form but largely extra-umbilical aperture. The development of a more globose, globigerine morphology with considerable umbilical extension of the aperture and prominent tooth is also seen as a secondary development in a number of lines, originating from both *Globorotalia* s.s. (= *Globorotaloides*) and from *Turborotalia* at different times (*Globoquadrina* and *Neogloboquadrina*) (Bandy *et al.* 1967).

Hantkeninacea

This superfamily includes Cenozoic genera with planispiral or streptospiral coiling modes and developing radially extended chambers or tubulospines and median apertures. Although homeomorphic with certain Mesozoic heterohelicaceans, the genera differ in detail from their earlier counterparts. Rugose to smooth forms with apertures that tend to extend into the apertural face or become areal are placed in the family Hantkeninidae. *Hantkenina* (plate 14) resembles *Schackoina* but has forward-directed tubulospines and different aperture. The Hastigerinidae includes spinose to smooth genera with triradiate spines at the periphery or at the ends of bulbous chambers. In *Hastigerina* the spines actually become barbed (Saito *et al.,* 1976). There are also clavate but smooth forms, *Clavatorella* and *Protentella,* which may represent a separate stock (Srinivasan and Kennett, 1975; Saito *et al.,* 1976).

POSSIBLE EVOLUTIONARY RELATIONSHIPS

Members of the Guembelitriidae with moderate trochospire first appear in the M. Jurassic in association with the Oberhauserellidae which is presently taken to include globigerine forms such as *Conoglobigerina.* A direct evolutionary progression from the Oberhauserellidae has been postulated (Loeblich and Tappan, 1974). Although it is possible that the Globigerinida arose directly from aragonitic ancestors, there is no direct evidence to support the idea and it seems unlikely. It is also possible that genera such as *Conoglobigerina* should be removed from the Oberhauserellidae, although Masters (1977) regards the aperture in this genus as 'atypical' for a planktonic form.

Guembelitria, which is high trochospiral with supplementary apertures and distinctive pore mounds, appears in the L. Cretaceous. Similar forms are present in the Palaeogene but differ in their rugose surface texture and may represent a separate subfamily.

The origin of the Hedbergellacea is also obscure but may represent an offshoot from *Caucasella* in the early L. Cretaceous (Hauterivian). Rapid evolution led to the appearance of clavate forms by the Aptian and keeled forms (*Praeglobotruncana*) by the Albian—see figure 14.1. The Rotaliporidae apparently arose directly from *Hedbergella,* via *Ticinella* in the late Aptian with the independent acquisition of a keel, as in *Rotalipora,* in the Albian. Some species show a tendency towards loss of the keel, *Anaticinella,* in the Cenomanian and Turonian. Maximum diversity was achieved in the Albian and Cenomanian. *Rotalipora* died out at the end of the Turonian and *Hedbergella* became relatively rare in the late Cretaceous before dying out in the Maastrichtian.

The prolific *Hedbergella* stock also gave rise to *Globotruncana* near the Cenomanian/Turonian boundary via species with globose chambers, imperforate peripheral band and with weak double keel sometimes present *(Archaeoglobigerina).* Evolutionary radiation took place rapidly in this group also, the family becoming extremely abundant world wide. Both single- and double-keeled species appeared, and flattened tabular forms (*G. linneana*) as well as moderately high, conical forms (*G. contusa*). In contrast to the decline of the other families a notable proliferation of globotruncanids took place in the late Cretaceous with the appearance of the highly ornamented *Rugoglobigerina,* probably from *Archaeoglobigerina,* in the late Santonian. This genus also gave rise to keeled forms (*Rugotruncana*) and clavate species (*Plummerita*) in the late Campanian and Maastrichtian. The origin of *Abathomphalus* is unknown but this group may

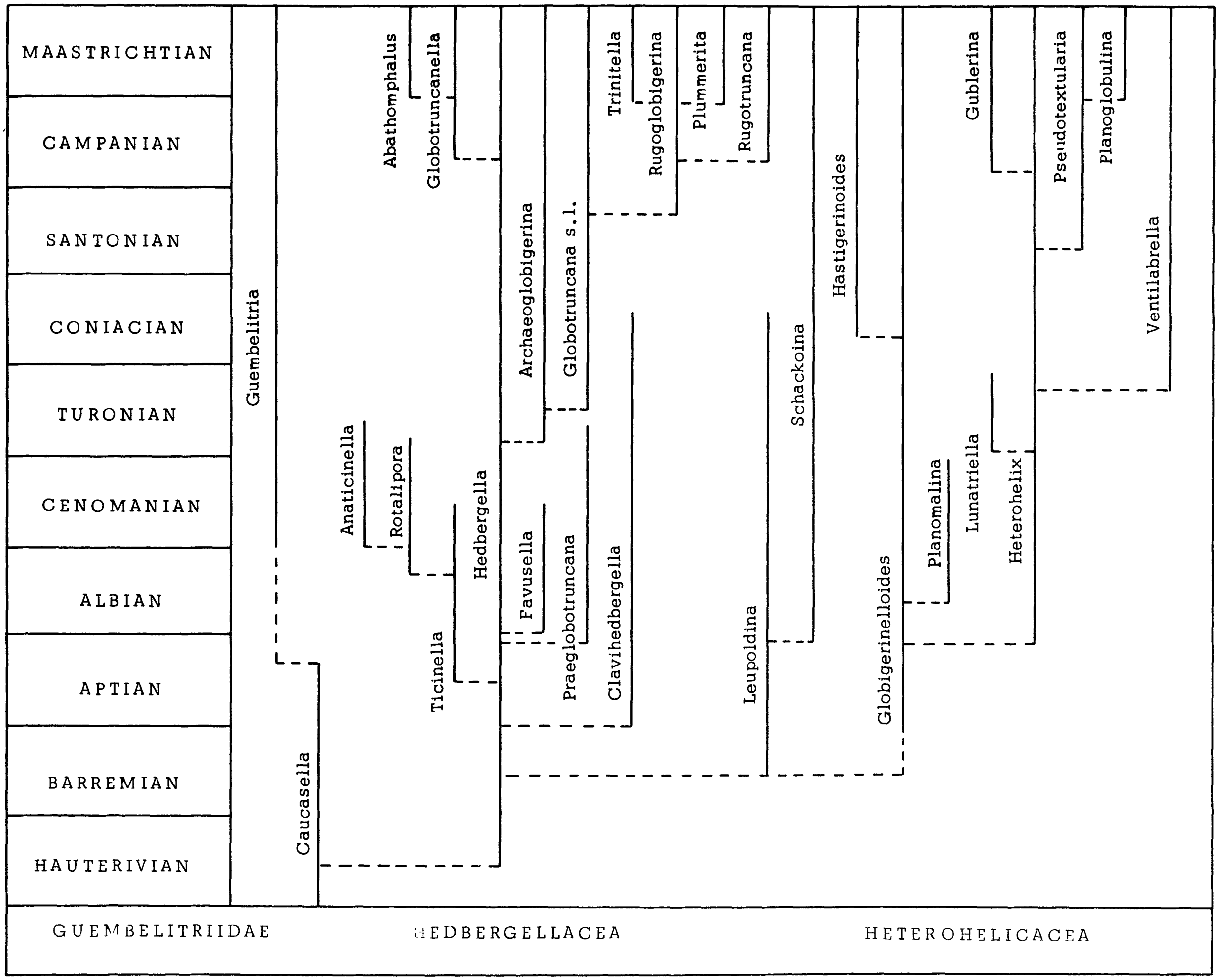


Figure 14.1 Evolutionary relationships among the Mesozoic Globigerinida, showing the ranges of important genera. After various authors

have arisen separately from *Hedbergella* in the late Santonian, via *Globotruncanella* (Longoria and Gamper, 1975).

The Planomalinidae (Heterohelicacea) apparently arose from *Hedbergella* via *Globigerinelloides* near the Barremian/Aptian boundary. Keeled forms (*Planomalina*) remained rare but appeared in the Albian. This family is most prolific and diverse during the Albian and Cenomanian but continued until the end of the Maastrichtian. *Hastigerinoides* arose from *Globigerinelloides* near the Turonian/Coniacian boundary and also continued until the Maastrichtian.

Leupoldina appeared as early as the Barremian so the Schackoinidae may have arisen separately, from *Hedbergella*. *Schackoina* appears in the Albian and is most prolific and diverse in the Cenomanian. *Leupoldina* died out in the Coniacian and only one species of *Schackoina* continued into the Maastrichtian.

The Heterohelicidae appear in the Albian, possibly derived from *Globigerinelloides*. Strikingly, *Heterohelix* and its spinose form, *Lunatriella,* remain virtually the only genera of this family present until the late Cretaceous. *Heterohelix* then gave rise to *Ventilabrella* in the late Turonian and *Pseudoguembelina* and *Pseudotextularia* in the Santonian. *Gublerina* appeared in the Campanian and *Planoglobulina* developed from *Pseudotextularia* in the Maastrichtian. This family, like the Globotruncanidae, therefore reaches its acme in the Campanian and Maastrichtian. The Chiloguembelinidae are the only family of heterohelicaceans to occur in the Tertiary and may have developed directly from *Heterohelix* near the Mesozoic/Tertiary boundary.

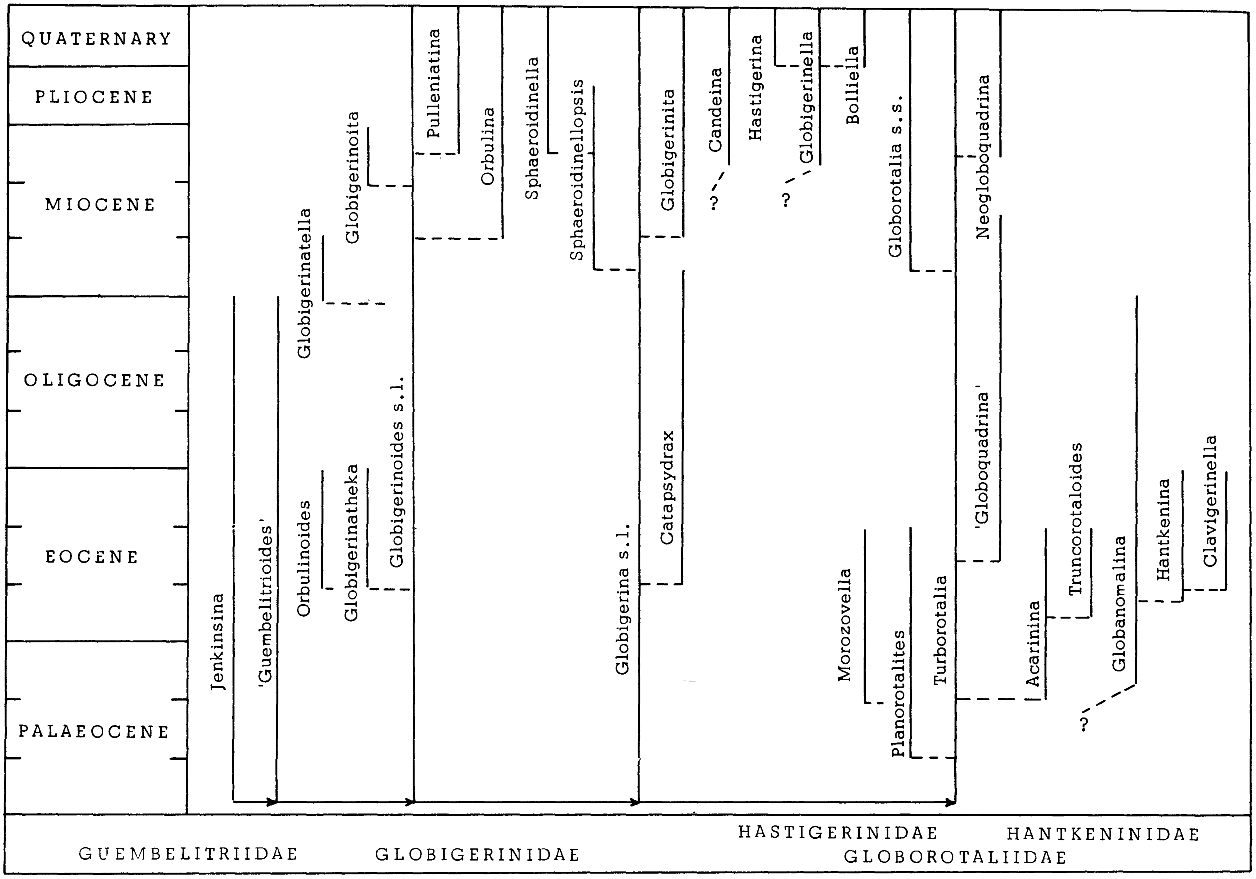


Figure 14.2 Evolutionary relationships among the Cenozoic Globigerinida, showing ranges of important genera. After various authors

A perusal of some of the latest evolutionary schemes for the Cenozoic Globigerinacea (Lipps, 1966; McGowran, 1968; El-Naggar, 1971; Jenkins, 1971a; Steineck, 1971; Loeblich and Tappan, 1974; Saito *et al.*, 1976; Berggren, 1977) reveals considerable disagreement. This is perhaps more apparent than real, being largely the result of the different emphasis put upon surface texture by the various authors in the attempt to overcome the problems of iterative evolution. This has resulted in uncertainty about the generic limits to be set for *Globigerina, Globigerinoides* and *Globorotalia* and especially about the position of *'Subbotina'*. Thus, those authors that favour removal of early Palaeogene species of *Globigerina,* as *Subbotina* to the 'Catapsydracidae' and species of *Globigerinoides* as *'Globoconusa'* to the Globorotaliidae (Lipps; Steineck; Loeblich and Tappan) consider the *Globigerinidae* made a late arrival on the Tertiary scene. This has led to the conclusion that the *Globorotaliidae* sprang directly from *Hedbergella* near the Mesozoic/Cenozoic boundary, giving rise almost immediately to the Catapsydracidae which in turn gave rise to *Globigerina* but not until the Eocene. Although other workers have retained *Subbotina* within the *Globigerinidae* it is still considered to have evolved from *Hedbergella* (as by Berggren) but to have given rise to both the Globorotaliidae and the Globigerinidae early in the Palaeocene. In contrast, *Subbotina* is suppressed altogether by El-Naggar and on the basis of the similarity and possible affinity between early Tertiary *'Guembelitria'* and *Globigerinoides* (noted by Olsson, 1970) he prefers the radical alternative of an origin within the Guembelitriidae.

As shown in figure 14.2, El-Naggar's suggestion is followed here but it must be admitted that there is as yet no real evidence available and the evolutionary studies necessary to trace the relationships of these enigmatic early forms remain to be done. Jenkins (pers. comm.) is 'reasonably convinced that all planktonic Foraminifera became extinct at the end of the Maastrichtian'.

The most striking evolutionary development in the early Palaeocene was the appearance of the spinose globorotaliids, probably stemming from *Turborotalia;* these include *Acarinina* and *Truncorotaloides,* together with relatively smooth forms homeomorphic with *Globorotalia* s.s. (*Planorotalites*) and angulo-conical forms with spinose keels, *Morozovella.* Planispiral genera also arose from this prolific stock, *Globanomalina* leading to *Hantkenina* with its peripheral tubulospines. Maximum diversity occurred in the Middle Eocene when bullate forms appeared in both the *Globigerina* and *Globigerinoides* lines together with a spherical test shape in *Orbulinoides.* Few of these genera survived the Palaeogene, most dying out at the end of the Eocene, but the relatively undifferentiated rootstocks crossed the Neogene boundary to give a proliferation of new genera in the Miocene. Both *Globigerina* and *Globigerinoides* apparently gave rise to new bullate forms (*Globigerinita* and *Globigerinatella*) as well as to smooth (*Sphaeroidinellopsis*) and globular embracing (*Pulleniatina*) and unilocular forms (*Orbulina*). The origin of *Candeina* is uncertain, but it may derive from *Globigerinita* (Parker, 1962; Blow, 1969). *Globorotalia* s.s. also appeared in the L. Miocene. Interestingly, although the bullate genera disappeared or declined at the end of the Miocene many of the other genera first appeared in the late Miocene and survived to the present. These include *Globigerinella* which gave rise to *Hastigerina, Bolliella* and the clavate *Hastigerinopsis* near the Quaternary boundary. *Clavatorella* appears to represent the parallel appearance of clavate chambers in a smooth-walled stock possibly derived from *Globorotaloides.* Plano-convex forms of *Globorotalia,* sub. gen. *Truncorotalia* also appear during the late Neogene.

ADAPTIVE TRENDS

These evolutionary developments may be interpreted as the result of adaptive trends, most of them exhibited to some degree by both Mesozoic and Cenozoic globigerinids in their attempt to exploit fully the possibilities of the planktonic realm. These trends include:

(1) From high to low trochospiral chamber arrangement with increasing overlap and globosity to give spherical test shapes. This is accompanied by an increase in number of apertures (or by appearance of 'spiro-umbilical' aperture coupled with partial detachment of the last chamber). The logical end point is reached in the perfect symmetry of *Orbulina* with even distribution of areal apertures and triradiate spines to support the vacuolated ectoplasmic envelope. This trend is best developed in the Globigerinidae but is also shown to a lesser extent by the Hedbergellacea.

(2) From low trochospiral to planispiral or streptospiral chamber arrangement, with migration of the aperture to the periphery. This may also give a globular test shape or the chambers become laterally extended or clavate. This trend is best developed in the Heterohelicacea and also in the Hantkeninacea which show a polyphyletic origin from at least three, both spinose and smooth, stocks.

(3) From globose, low trochoid to truncate or keeled tests. This trend is well developed in the Hedbergellacea (with double keels in the Globotruncanidae) and in at least two separate lines of Globorotaliidae.

(4) Towards the development of apertural and umbilical coverplates by coalescence of umbilical teeth (Hedbergellacea) and by the appearance of discrete bullae in the Globigerinidae. The parallel development of umbilical teeth occurs in at least three stocks of Globorotaliidae and also, less strongly, in the Globigerinidae. It apparently leads to the formation of a true coverplate only in the case of *Clavatorella,* where it resembles a 'webbed foot' (Saito *et al.,* 1976).

(5) Towards the development of a rugose test surface with growth of euhedral calcite rhombs. The trend is strongly expressed in the Hedbergellacea and also in the Globorotaliidae where the ornament is often developed to the point of becoming a 'secondary crust'.

Trends detected only in Cenozoic families include: (a) the development of long, detachable spines in the Globigerinacea, especially in the Globigerinidae where they become triradiate, and in the Hastigerinidae where they become both triradiate and barbed; (b) the development of countersunk pores with funnel-shaped or flat-bottomed pits, linked with the appearance of reticulate or cancellate ornament in the Globigerinacea.

Trends detected only in Mesozoic families include: (a) the move from planispiral to biserial and spreading chamber arrangement—this is shown only in the Heterohelicacea and is linked with the dominance of longitudinal costation, although the Chiloguembelinidae could represent a separate Tertiary line; (b) the development of raised ridges in a polygonal pattern, as well as meridional costellae, in the Hedbergellacea.

The adaptive significance of these morphological trends is underlined by the correlation between the four major radiations of the globigerinids (well shown in figures 14.1 and 14.2) and major oceanic episodes during the Albian/Cenomanian interval, the late Senonian and Maastrichtian, the late Palaeocene and Eocene and during the Miocene. These great transgressions with consequent climatic amelioration created stable environments and promoted maximum niche colonisation (Tappan and Loeblich, 1973b).

APPLICATION IN STRATIGRAPHY

The marked evolutionary changes shown by the Globigerinida through the late Mesozoic and in the Cenozoic make this group valuable in biostratigraphy at both the family and generic level, with a number of 'datum lines' discernible, figure 1.3 (see below for a discussion of datum horizons which are not all of equal importance or necessarily isochronous).

The Lower Cretaceous is characterised by appearance and dominance of Hedbergellidae, Rotaliporidae and Schackoinidae. Important datum lines are provided by the appearance of *Leupoldina* and *Schackoina* near the Barremian/Aptian boundary, the appearance of *Rotalipora* near the Albian/Cenomanian boundary and by its extinction in the early Turonian.

The Upper Cretaceous is marked by the dominance of Globotruncanidae and Heterohelicidae. Datum lines include the appearance of *Globotruncana* s.l. in the late Turonian, the appearance of *Rugoglobigerina* near the Santonian/Campanian boundary and the extinction of globotruncanids at the end of the Maastrichtian.

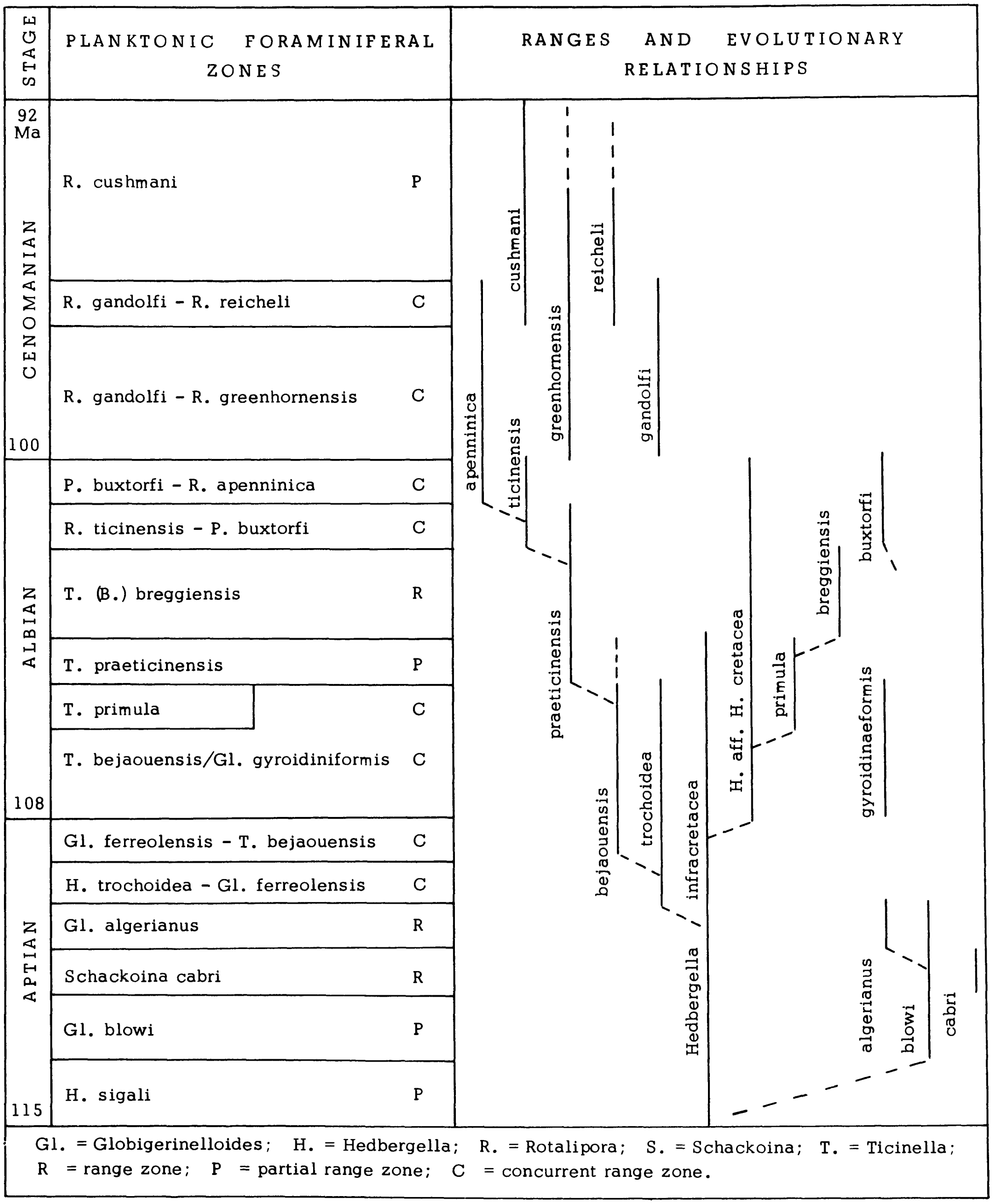
The Palaeogene is marked by dominance of the Globigerinidae, Globorotaliidae and Hantkeninidae. Datum lines can be drawn upon the appearance of *Globanomalina* near the Palaeocene/Eocene boundary, the appearance of *Hantkenina* at the Lower/Middle Eocene boundary and the extinction of *Acarinina* at the Middle/Upper Eocene boundary. *Globigerinoides* also appears in abundance near the Palaeogene/Neogene boundary.

As we have seen, a considerable proliferation of bullate and spherical Globigerinidae occurred in the Miocene with the appearance of a second wave of smooth globorotaliids. Notable datum lines are the 'Orbulina Surface' near the Lower/Middle Miocene boundary, the appearance of *Candeina* near the Middle/Upper Miocene boundary and the appearance of *Pulleniatina* in the Upper Miocene.

The Hastigerinidae rose to abundance in the late Cenozoic, and datum lines are provided by a sharp coiling change in *Pulleniatina,* the extinction of *Sphaeroidinellopsis* near the Zanclian/Piacenzian boundary and the appearance of *Globorotalia truncatulinoides* near the Pleistocene boundary.

As pointed out in chapter 1, the revolutionary impact of planktonic foraminiferal studies on inter-regional correlations in the last two decades stems largely from the work of Grimesdale (1951) who observed that the order of appearance and disappearance of certain planktonic species was the same in the Palaeogene of the Caribbean and the Middle East, although Glaessner (1937) did pioneer work on Palaeogene planktonics from the Caucasus and in his textbook (1945, see reprint 1963a) emphasised the stratigraphical importance of the species of the planktonic genera *Hantkenina* and *Globotruncana.* The usefulness of *Orbulina universa* as a Middle Tertiary indicator was also suggested by Leroy as early as 1948. This pioneer work led to comprehensive studies in Russia (Subbotina, 1953, see 1971 translation; Khalilov, 1956; Morozova, 1959) and in the Caribbean (Brönnimann, 1952a, 1952b; Gandolfi, 1955; Weiss, 1955; Bolli, 1957a, 1957b, 1957c; Loeblich *et al.,* 1957; Blow, 1959). It was found possible to zone much of the Tertiary succession in Trinidad on the basis of planktonic index species, thus differentiating some thick sequences of shales, and then to trace these zones throughout the Gulf Coast Region and Central America.

Successful application in the Caribbean sparked off similar studies on the Cenozoic all round the world during the next decade. These include: California (Lipps, 1964); the Pacific (Parker, 1962, 1964, 1967); Philippines (Bandy, 1963); Japan (Asano, 1962; Saito, 1962, 1963); Papua (Belford, 1962); the Solomons (McTavish, 1966); Australia (Jenkins, 1960); New Zealand (Jenkins, 1964, 1965); Egypt (El-Naggar, 1966); Italy (Luterbacher, 1964; Cita, Premoli Silva and Rossi, 1965; Barbieri, 1967, 1969; Bertelino, 1968); Central Europe (Gohrbandt, 1963); Denmark (Troelsen, 1957; Berggren, 1960); Holland (Hofker, 1962). On this basis, tentative efforts were made to build up a 'worldwide' zonal scheme (Bolli, 1959; Stainforth, 1960; Bandy, 1964; Jenkins, 1965, 1966) leading eventually to Blow's correlation table (1969) with some 40 numbered zones for the Palaeogene and Neogene. An equivalent burst of activity on the Cretaceous planktonics (Klaus, 1960; Barr, 1962; Ollson, 1964; Bolli, 1966; Moullade, 1966; El-Naggar,



Gl. = Globigerinelloides; H. = Hedbergella; R. = Rotalipora; S. = Schackoina; T. = Ticinella;
R = range zone; P = partial range zone; C = concurrent range zone.

Figure 14.3 Early Cretaceous planktonic foraminiferal zones and evolutionary relationships. After Hinte (1976) and based on numerous authors

1966; Bandy, 1967; Sigal, 1967; Pessagno, 1967, 1969) also led to the production of a worldwide correlation scheme (Hinte, 1972). These advances in inter-regional correlation fortunately coincided with the beginning of the Deep Sea Drilling Project, which meant that a standard zonation could immediately be applied. This has further accelerated the increase in planktonic studies and hundreds of papers have appeared detailing the results, both in the 50 volumes of 'Initial Reports' which have already appeared and in various journals—see Zobel (1975) and under Further Reading at the end of this chapter.

The flood of information from the deep ocean basins has led to refinements of the correlation tables. In particular, Blow's scheme was found difficult to apply outside tropical regions and parallel schemes for high latitudes have been developed (Jenkins, 1971a, 1975, 1978a; Berggren, 1972a), together with a simplified table of zones for worldwide correlation (Stainforth *et al.*, 1975). Further developments still being pursued have been the correlation of the planktonic foraminiferal zones with those erected on the

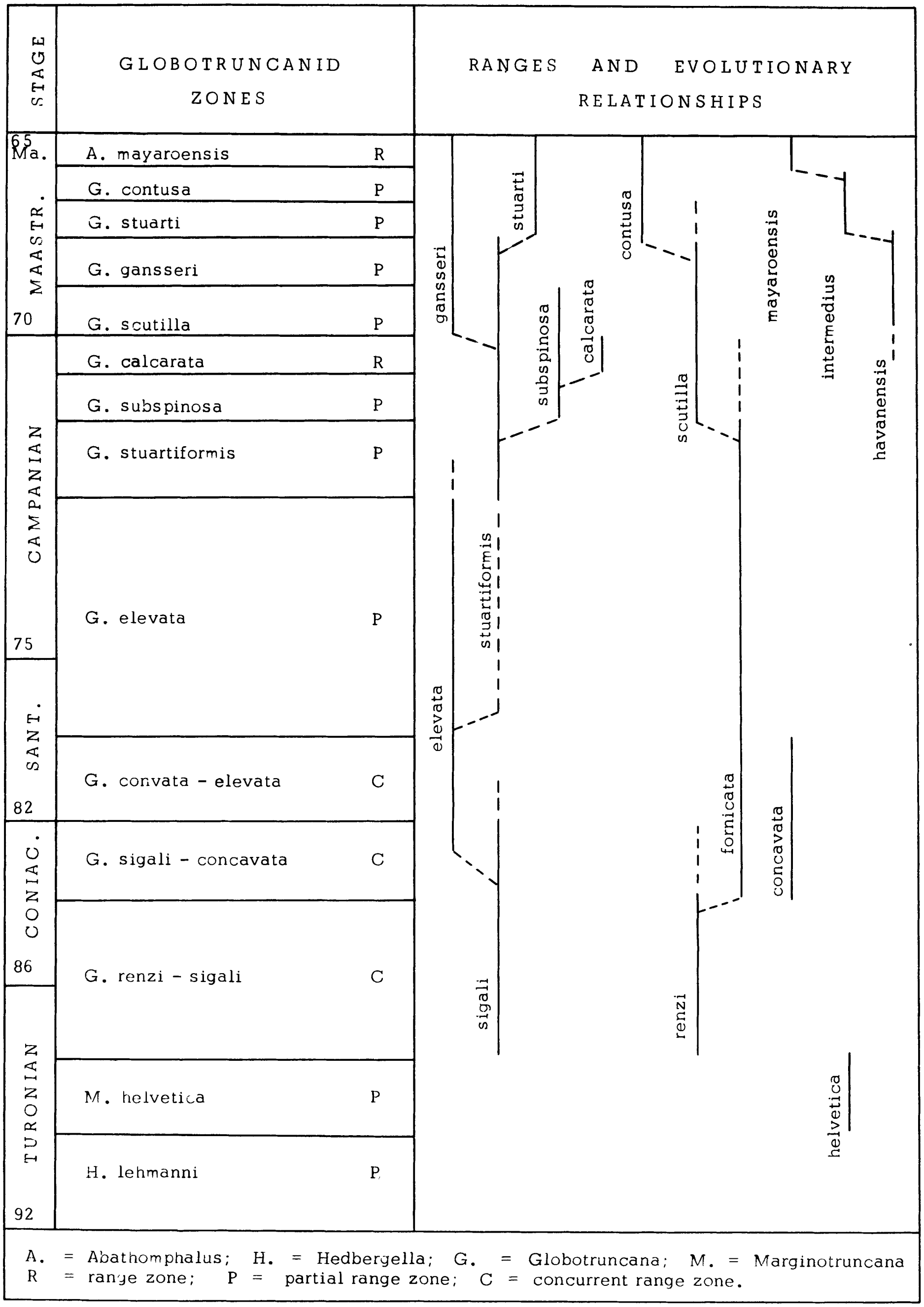


Figure 14.4 Late Cretaceous planktonic foraminiferal zonation and evolutionary relationships. After Hinte (1976) and based on numerous workers

basis of the nannoplankton (coccoliths, discoasters, diatoms, radiolaria and silicoflagellates) and with the radiometrically dated sequence of normal and reversed palaeomagnetism (Berggren, 1972b; Berggren and Couvering, 1974; Hinte, 1976; Couvering and Berggren, 1977; Wonders and Verbeek, 1977; Berggren, 1978; Berggren *et al.*, 1978). The standard zones for the Cretaceous, drawn from Hinte (1976), are shown in figures 14.3 and 14.4 and the zones for the Cenozoic, taken from Berggren (1978) and Stainforth *et al.* (1975), are shown in figures 14.5 and 14.6.

AGE M.Y.	EPOCH	STAGE	PALAEOGENE PLANKTONIC FORAMINIFERAL ZONATION: TROPICAL ATLANTIC		PALAEOGENE PLANKTONIC FORAMINIFERAL ZONATION: WORLDWIDE
25	22.5 OLIGOCENE	CHATTIAN	22 Globigerina angulisuturalis	P	Globigerina ciperoensis
			21 G. angulisuturalis/ Globorotalia opima opima	C	Globorotalia opima opima
30		RUPELIAN	20 Globigerina ampliapertura	P	→
			19 Globoquadrina sellii/ Globanomalina barbadoensis	C	Globanomalina micra C
35	37	LATTORFIAN	18 Globigerina tapuriensis	C	
	EOCENE	BARTONIAN	17 Catapsydrax gortanii/ Globorotalia centralis	P	Globorotalia cerroazulensis sensu lato P
40			16 Cribrohantkenina inflata	R	
			15 Globigerinatheka mexicana	P	Globigerinatheka semiinvoluta
		LUTETIAN	14 Truncorotaloides rohri	P	→
45			13 Orbulinoides beckmanni	R	→
			12 Globorotalia lehneri	P	→
			11 Globigerinatheka kugleri	C	Globigerinatheka subconglobata
			10 Hantkenina aragonensis	P	→
50		CUISIAN	9 Acarinina densa	P	Globorotalia pentacamerata
			8 Globorotalia aragonensis	C	→
			7 Globorotalia formosa	P	→
	54		6 Globorotalia subbotinae	P	→
55	PALAEOCENE	THANETIAN	5 Globorotalia velascoensis	P	→
			4 Globorotalia pseudomenardii	R	→
60			3 Globorotalia pusilla/ Globorotalia angulata	C	Globorotalia pusilla P Globorotalia angulata P
		DANIAN	2 Globorotalia uncinata	P	→
			↑ Globorotalia compressa	P	Globorotalia trinidadensis
			Globorotalia triloculinoides	P	Globorotalia pseudobulloides
65			1 Globigerina eobulloides	R	Globigerina eugubina

C = concurrent range zone; P = partial range zone; R = range zone (biozone)

Figure 14.5 Comparison of planktonic foraminiferal schemes for the Palaeogene of the tropical Atlantic (after Berggren, 1978), with numbers following Blow (1969) and the worldwide scheme of Stainforth *et al.* (1975). Note that *Globigerina* and *Globorotalia* are interpreted in the wide sense

AGE m.y.	EPOCH	STAGE	LATE CENOZOIC PLANKTONIC FORAMINIFERAL ZONATION	
			TROPICAL ATLANTIC	WORLDWIDE
	QUAT.		23 Globigerinella calida/ Sphaer. dehiscens excavata	Globorotalia tumida P
		CALABRIAN	22 Globorotalia truncatulinoides P →	
2	PLIOCENE	PIACENZIAN	21 Globorot. tosaensis tenuitheca C	Pulleniatina obliquiloculata P
			20 Globorotalia multicamerata/ Pulleniatina obliquiloculata C	
		TABIANIAN	19 Sphaeroidinella dehiscens/ Globoquadrina altispira P	Globorotalia margaritae R
5			18 Sphaeroidinellopsis subdehiscens/ Globorotalia tumida P	
	MIOCENE	MESSINIAN	17 Globorot. tumida plesiotumida C	Globorotalia acostaensis P
		TORTONIAN	16 Globorotalia acostaensis Globorotalia merotumida P	
10		SERRAVALLIAN	15 Globorotalia continuosa C	Globorotalia menardii P
			14 Globigerina nepenthes/ Globorotalia siakensis P	Globorotalia siakensis
			13 Sphaeroidinellopsis subdehiscens/ Globigerina druryi P	
			10-12 Globorotalia fohsi gr. R	G. fohsi lobata, fohsi robusta G. fohsi fohsi
15		LANGHIAN	9 Orbulina suturalis/ Globorotalia peripheroronda P	Globorotalia peripheroronda
			8 Globigerinoides sicanus Globigerinatella insueta P	Praeorbulina glomerosa
		BURDIGALIAN	7 Globigerinatella insueta/ Globigerinoides quadrilobatus trilobus P	Globigerinatella insueta
			6 Globigerinatella insueta/ Catapsydrax dissimilis C	Catapsydrax stainforthi
20		AQUITANIAN	5 Globoquadrina dehiscens/ G. dehiscens praedehiscens P	Catapsydrax dissimilis
22.5			Globigerinoides quadrilobatus primordius/ 4 Globorotalia kugleri C	Globorotalia kugleri

C = concurrent range zone; P = partial range zone; R = range zone (biozone)

Figure 14.6 Comparison of planktonic foraminiferal schemes for the Neogene and Quaternary of the tropical Atlantic (after Berggren, 1978), with numbers following Blow (1969) and the worldwide scheme of Stainforth *et al.* (1975). Note that *Globigerina* and *Globorotalia* are interpreted in the wide sense. Tabianian = Zanclian and Piacenzian includes the Astian

PROBLEMS OF CORRELATION

As can be seen from the tables, a complete sequence of planktonic foram zones has been recognised from the Lower Cretaceous to the Holocene. These zones have been applied to biostratigraphy (more especially in the deep ocean) with success and increasing confidence. But this very success has its problems in that it has led some authors to make unwarranted claims for the universal worldwide applicability of the zones and for their unique value compared with other sorts of palaeontological criteria and to overlook that a number of unsubstantiated assumptions are involved.

The zones are based largely upon the successive appearances of selected index species. Thus the zone of *Hedbergella sigali* (figure 14.3) is based upon the partial range of that taxon from its appearance at the beginning of the Barremian to the appearance of *Globigerinelloides blowi*. The *Schackoina cabri* zone is based on the full range of the index species (biozone), the extinction level coinciding with the appearance of *Globigerinelloides algerianus*. However, the zone of *Rotalipora gandolfi-reicheli* in the Cenomanian is based on simple overlap of the two species (concurrent range zone) and the top of the zone rests solely on the disappearance and apparent extinction of *R. gandolfi*. The base of the *Rotalipora cushmani* partial range zone is also founded on this extinction level.

It is assumed that the appearance of such planktonic species in widely separate areas is a result of rapid evolution and geographical dispersal ('geologically instantaneous') and that these horizons are therefore reliable for correlation. Constant vertical order of the zones in different regions and agreement with other data seems to bear this out, at least within the broad latitudinal provinces. However, extinctions, unless brought about by rapid competitive exclusion, are likely to be locally variable, having according to Blow (1970), 'a considerable degree of in-built diachroneity'. Thus at the present time *Globigerina hexagona* still survives in the Indo-Pacific region although it has been extinct since the Pleistocene in the Atlantic. Both Blow (1970) and Jenkins (1971b) conclude that extinction levels should be avoided and certainly not dignified as 'datum planes', unless coincident with general palaeontological events, as is the extinction of the globotruncanids. However, the list of 42 datum planes given for the Neogene of the Pacific (Saito, 1977) still includes 20 extinctions.

Jenkins (1973a) also points out that first appearances of species of unknown ancestry (cryptogenes) may be diachronous to various degrees even within the Tropical Belt; thus *Globoquadrina dehiscens* appeared in the Oligocene in New Zealand and did not reach Trinidad until the Lower Miocene. He is also strongly critical of the 'blanket assumption' that most planktonic species have a truly worldwide range. Some authors have assumed that the strongly marked provincialism of present-day faunas is largely a late Cenozoic phenomenon brought about by increasing frigidity at the poles. But it is now known that there was a considerable expansion of Antarctic ice in the Upper Miocene and that valley glaciers existed in Antarctica as early as the Eocene. It is perhaps, therefore, not too surprising that certain species were restricted to the tropics in the Eocene, while others like *Hantkenina alabamensis* made only a brief incursion into New Zealand during the U. Eocene. *Globigerinatella insueta* appears only once in New Zealand and conversely there are species that are restricted to the austral region.

Nor can provincialism be solely ascribed to temperature controls because at the present time *Globorotalia truncatulinoides* is primarily found in cold water in the southern oceans but occurs in warm water in the northern oceans. This helps to explain why out of 29 datum planes recognised by Berggren (1969b) six could not be traced in N. Zealand, while in 19 the index taxa are very rare. Of the ten that could be properly determined, five were considered diachronous by Jenkins and five isochronous, these last including the globotruncanid extinction, the *Globanomalina, Globigerinoides* and *Orbulina* datums and the appearance of *Globigerina nepenthes,* although even the *Globigerinoides* datum is considered diachronous by Lamb and Stainforth (1976). Figures 14.5 and 14.6 show rather well that 'worldwide' correlation is best achieved (with least modification of Blow's zones) during the Eocene and M. Miocene climatic optima, and also during the Palaeocene when there was rapid evolution into empty ecologic niches.

As we have noticed in the case of most other groups of Foraminifera, the difficulties presented by 'empirical index fossils' have led to considerable activity in the attempt to differentiate steps in evolving lineages. Figures 14.3 and 14.4 show that this work has met with some success in the Cretaceous, with analysis and application of the *Hedbergella cretacea* group in the Lower Cretaceous and the *Globotruncana sigali* and *G. renzi* groups in the Upper Cretaceous. However, the origin of a large number of species is still unknown, especially in the Aptian, Cenomanian and Turonian. Also it has to be admitted that the evolutionary schemes are tentative, somewhat subjective, being largely based on circumstantial evidence, and not backed up by statistical study of variation through continuous sections (on the lines of Kuhry *et al.*, 1977).

Examples of similar studies in the Cenozoic include: in the Palaeocene and Eocene, the *Acarinina/Truncorotaloides* lineage (Berggren, 1969b) and the *Globorotalia chapmani/Globanomalina wilcoxensis* lineage (Berggren, Ollson and Reyment, 1967); and in the Miocene, the *Globorotalia (Turborotalia) praescitula – praemenardii* lineage (Blow, 1959, 1969; Jenkins, 1971a, 1973a), the *Globorotalia* (*T.*) *peripheroronda – Globorotalia* (*G.*) *fohsi* lineage (Bolli, 1950, 1957b, 1967; Banner and Blow, 1966; Blow, 1969), and the *Orbulina* lineage (Blow, 1956; Jenkins, 1960) described earlier—see figure 5.2. However, as in the case of the Cretaceous examples, the statistical methods introduced by Scott (1966, 1967, 1969, 1971, 1976) have not been employed, so a similar uncertainty surrounds them. Indeed, as has been found with Larger Foraminifera, the time element is a bar to this sort of study (Jenkins, 1971b). In addition, the problem of differing rates of evolution, with branch lines and iterative development in different water masses, occurs in this group as well (Jenkins, 1973a).

The line *Globorotalia (Turborotalia) peripheroronda – G. (T.) peripheroacuta – G. (G.) praefohsi – G. (G.) fohsi* is reliable in the tropics but in the subtropics and in the cooler austral region *G. (T.) peripheroronda* persists longer and gives rise to *G. (T.) mayeri* as a separate line (Jenkins, 1960). *Globorotalia (G.) crassula conomiozea* apparently develops repeatedly from *G. (T) crassaformis* with 'random' acquisition of a keel (Blow, 1970). Again, in the tropics, *Globorotalia (T.) praescitula* gives rise to *G. (G.) archaeomenardii – G. (G.) praemenardii – G. (G.) menardii.* But in New Zealand *G. (T). praescitula* gives rise to the branchline *G. (G.) praemenardii – G. (G.) miotumida,* as well as to encrusted forms of *G. (G.) praemenardii, = G. (G.) miozea.* Thus, not only are there branchlines which evolved at different rates but there is strong evidence that the acquisition of a keel (*Globorotalia* s.s.) relates to climatic factors, especially warmer water.

In practice then, the tables of standard zones are based mainly upon empirical index species, supplemented by abundant species of joint occurrence. The zones are therefore, to a large extent, also assemblage zones (faunizones), exactly as in traditional biostratigraphy—see discussion of zones in Stainforth *et al.* (1975). The thought that a fully phylogenetic zonal scheme will eventually be produced is checked by the observation that cryptogenes appear to be general, as is to be expected if allopatric speciation is the rule. As explained in chapter 5, the lineages mentioned could be rare examples of sympatric speciation but are more likely to represent a form of allopatric speciation with the subspecies adapted to different water layers and only brought together on death. It is significant that all these lineages developed during either the Palaeogene or Miocene climatic optimum, when the water column was most differentiated, especially in the Miocene with the full development of the cold, bottom layer (psychrosphere). Normally, it is probable that subspecies adapt to different water masses and become widely separated laterally also. However, one possible origin for cryptogenes is in the largely unanalysed species of less than 75 μm diameter.

A further limitation on the possibility of tracing lineages vertically is the discovery of 'unexpectedly widespread' erosion intervals and non-sequences in deep-sea sediments (Carter and Landis, 1972; Kennett *et al.*, 1972; Rona, 1973; Sigal, 1974). These hiatuses are related to plankton productivity and removal of bottom sediments by dissolution or strong and corrosive bottom currents, changes in the shape of the oceans and circulation patterns having a major effect on balance and erosion (Moore *et al.*, 1978). As might be expected, the major unconformities occur at the Era and System boundaries but the breaks near the Middle/Upper Miocene boundary (probably related to growth of the Antarctic Ice Cap) are apparently more marked than at the Oligocene/Miocene boundary. Interestingly, in view of what has been said above, the least breaks and most continuous sections occur in the Lower and Middle Eocene and Lower and Middle Miocene.

The different susceptibility to solution of particular species deposited at depths near the CCD (below the 'lysocline' which marks the onset of marked solution effects, some hundreds of metres above the CCD, at about 4000 m, but much shallower in the Antarctic) is also a problem (Berger, 1967, 1970). This has been partially solved by the erection of parallel zonal schemes based on the more resistant species (Jenkins and Orr, 1971; Orr and Jenkins, 1977). Also, on the positive side, it must be pointed out that the detection of non-sequences by accurate planktonic foram zonation and of periods of deepening by noting selective solution effects below the lysocline has proved of prime value in unravelling the historical development of the oceans (Berger, 1972, 1975; Berger and Winterer, 1974; Andel *et al.,* 1975, 1976, 1977).

Another restriction on the 'worldwide' application of the zones is the comparative rarity of planktonic forams in turbid, shallow shelf waters. As mentioned, the Globigerina Ooze generally commences on the lower Continental Slope. Although dead shells may drift for a considerable time after death (Boltovskoy and Wright, 1976) and may even occur in estuarine deposits (Haynes *et al.,* 1973) the average settling rate is 1 cm/s (Berger and Piper, 1972), which means that unless retarded by turbulence dead tests reach the deep-sea floor in a few days. Most dead tests are therefore deposited on the sea bed below the surface water where the Foraminifera lived, no doubt helped by the development of heavy calcite crusts in some species after gametogenesis (Bé, 1977). This was realised long ago by Murray (1897) who also noted the build-up of Globerigina Ooze at the convergence of water masses. In these circumstances, although high numbers of drifted specimens may occur on the outer shelf, penetration of the inner shelf is usually impersistent and uncertain.

Zonation of Cretaceous and Cenozoic, inner-shelf sediments therefore still depends largely on the benthonic species. Lateral correlation into deep water has to be made using alternative groups according to environment. This approach, involving integrated analysis of different groups, was pioneered by Henson (1950b) in his studies in the Kirkuk oilfield in Iraq. Here the Tertiary rocks show the typical lateral facies variation found in most parts of the Middle East and North Africa. These facies are related to the pattern of submerged platforms and tectonic basins developed along the drowned margins of the Afro-Arabia foreland during its northern drive towards Asia. The land areas to the south were generally low, and little terriginous material was brought into the gulfs. Under these conditions Larger Foraminifera, as well as algae, bryozoans and corals, flourished in the shoal areas and as a result, fossil fragmental limestones and marls dominate the lithological sequence.

The dominant sediments in the basins are Globigerina marls, often up to 3000 m thickness, interdigitating with the reefal and shelly foraminiferal limestones over the platforms and towards the shore. Where definite reefs were formed at the edges of the platforms, lagoons were created behind them, often with precipitated chemical limestones. In other profiles true reef was absent and reefal shoals occurred with more open lagoonal or littoral conditions behind them. All these sedimentary environments were developed in the Sirte Basin in Libya, and figure 14.7 shows how the typical foram facies associated with them can be cross-correlated on the basis of different groups and related to the standard time scale.

It is amusing and revealing to recall that when I began work in Libya, it was suggested that I could as well do all my work in a laboratory in New York or London. That is, if I relied on air-mailed samples and concentrated on the planktonic forams. However, by paying equal attention to both large and small benthonics as well as planktonics, together with bivalves, echinoids and corals, collected when out with the field parties, I was able to apply an overall facies analysis to the west flank of the Sirte Basin on the lines of Henson's work. There is no doubt that, by taking this eclectic approach, I was able to make a much greater contribution than I otherwise could have done to the team effort that led to the discovery of the Zelten Field.

In the light of all these observations it is obvious that the student should be very wary of those authors who, carried away by the success of planktonic foram zonation in relatively deep water, have suggested that the zones should replace the international stages and be made the basis of direct 'chronologic' subdivision of the epochs. However, if the epochs, such as Eocene and Miocene, are to be retained it is clear that they cannot stand without the basis of their constituent stages, also that the stages should be founded on general evolutionary events. As we have seen, replacement of the stages by 'datum planes' is open to grave objection. Again, there seems little advantage in avoiding the use of stage names yet dividing the epochs into early, middle and late, because inevitably as in Berggren's tables (Berggren, 1978), these divisions become directly equated with the stages, as indeed they should be. It seems a little odd that workers should baulk at recognising the stages internationally but accept the 'worldwide' provenance of zones which may, in certain areas, lack the characteristic index species. It must be kept in mind that zones are flexible, informal biostratigraphical units that are subject to revision as our knowledge of the ranges of the particular index fossils improves. Stages are formal chronostratigraphical units based on selected type sections and although there may be disagreement about their precise boundaries they are fairly static and rigid in application.

The student should also appreciate that although radiometric dates support the relative

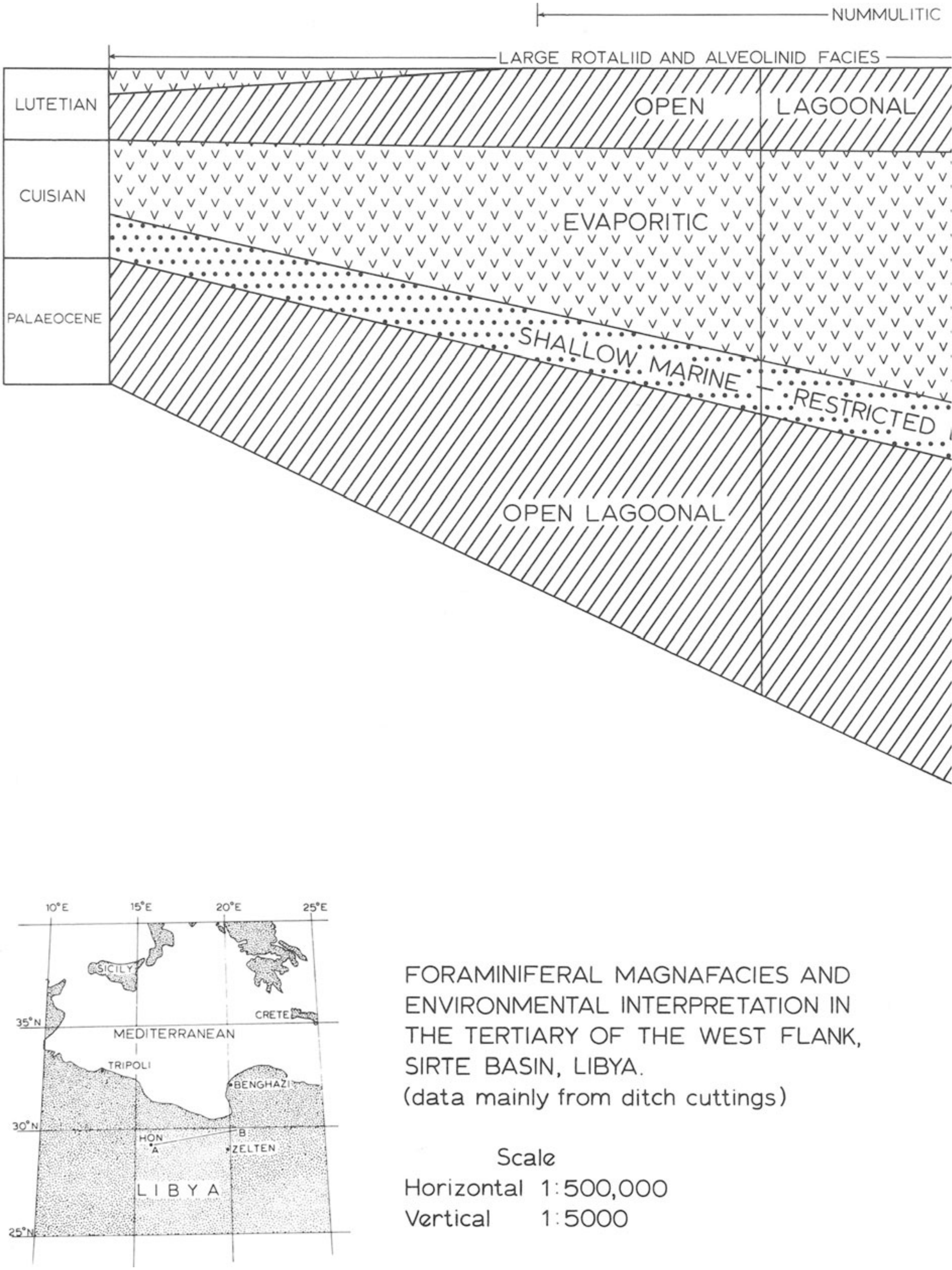
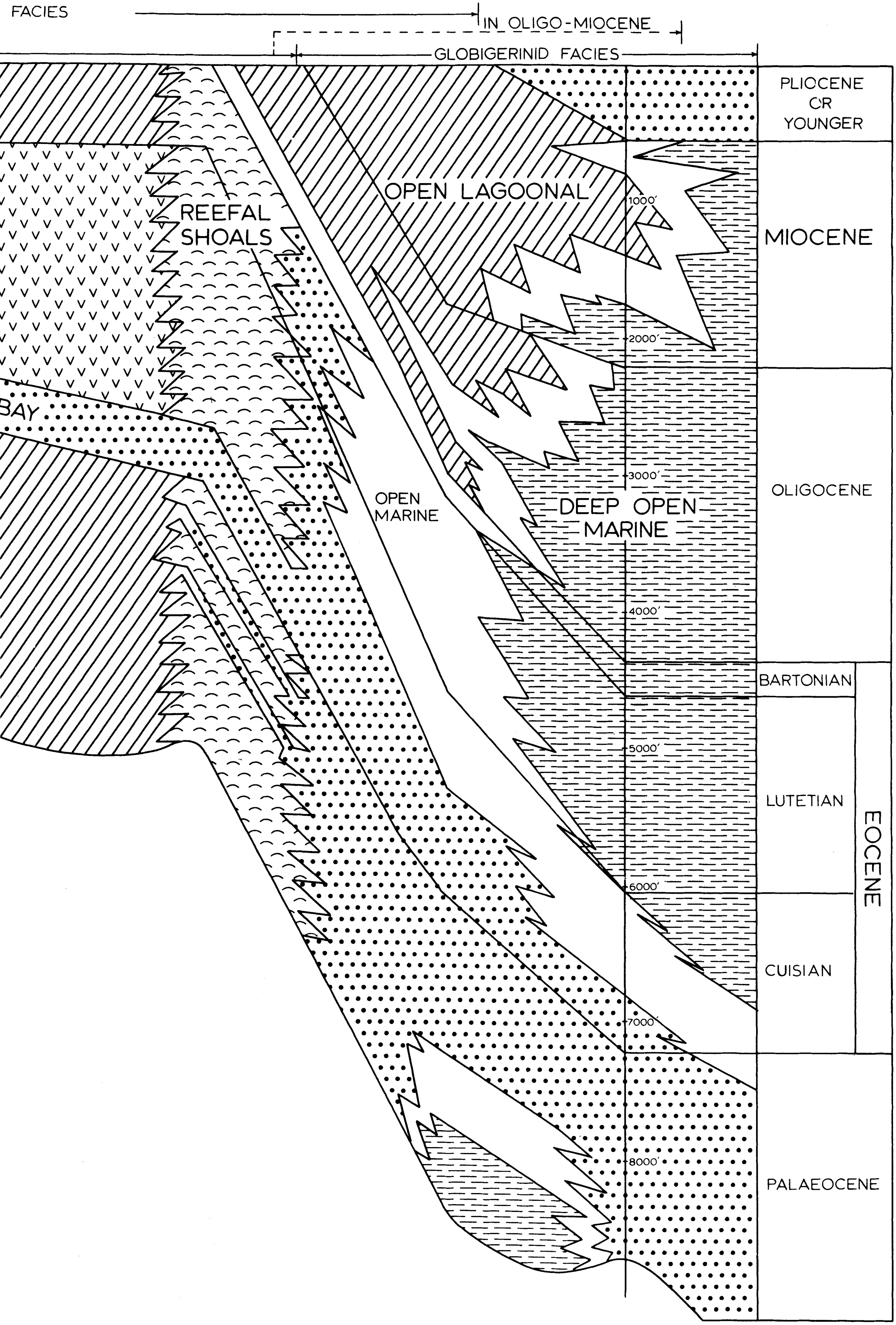

NUMMULITIC
LARGE ROTALIID AND ALVEOLINID FACIES
LUTETIAN
CUISIAN
PALAEOCENE
OPEN
LAGOONAL
EVAPORITIC
SHALLOW MARINE – RESTRICTED
OPEN LAGOONAL
10°E
15°E
20°E
25°E
35°N
30°N
25°N
SICILY
CRETE
MEDITERRANEAN
TRIPOLI
BENGHAZI
HON
A
B
ZELTEN
LIBYA
FORAMINIFERAL MAGNAFACIES AND ENVIRONMENTAL INTERPRETATION IN THE TERTIARY OF THE WEST FLANK, SIRTE BASIN, LIBYA.
(data mainly from ditch cuttings)
Scale
Horizontal 1:500,000
Vertical 1:5000

Figure 14.7 Foraminiferal magnafacies in the Tertiary of the west flank, Sirte Basin, Libya


FACIES
IN OLIGO-MIOCENE
GLOBIGERINID FACIES
PLIOCENE OR YOUNGER
MIOCENE
OLIGOCENE
BARTONIAN
LUTETIAN
CUISIAN
EOCENE
PALAEOCENE
OPEN LAGOONAL
REEFAL SHOALS
BAY
OPEN MARINE
DEEP OPEN MARINE
1000′
2000′
3000′
4000′
5000′
6000′
7000′
8000′

positions of the stages, the inherent imprecision of the potassium/argon method employed on glauconites means that there is an error of about two million years in the Palaeogene and up to five million years or more in the Cretaceous. The resolution of the zones, which apparently average about 1.5 m.y. length, is of course much greater. Even in the Neogene, where the error is less than 1 m.y. and calibration of the polarity sequence most firmly established, attempts to date the Pliocene/Quaternary boundary in the Mediterranean have run into great difficulty. This is apparently because of post-depositional precipitation of magnetic materials and overprinting by normal geomagnetism in the last half-million years (Watkins, Kester and Kennett, 1974). There is also the problem of the recycling of glauconite grains, which is especially likely at the beginning of sedimentary cycles.

ECOLOGY

The first suggestion that the mode of life of the globigerinids might be planktonic was made by Owen (1867) and amply confirmed during the voyages of the research vessel 'Challenger' during 1872 – 76 (Brady, 1884). It then became clear that, although drifting passively at the mercy of the currents, they occur in global, latitudinal belts, with most species in the tropics and only a few in cold water. This suggested that water temperature was the most important factor in their distribution pattern (Murray and Renard, 1891; Murray, 1897). Other pioneer investigations at this time were those of Pearcey (1890), in the North-west Atlantic, and those made by Rhumbler (1901, 1911).

Modern studies of distribution both in bottom sediments and from tow nets include: North Atlantic (Phleger *et al.,* 1953; Bé, 1959, 1960; Bé and Hamlin, 1967; Cifelli, 1962, 1965, 1967; Ruddiman, 1969; Barash, 1971; Bé and Tolderlund, 1971; Imbrie and Kipp, 1971; Cifelli and Smith, 1969, 1974; Balsam and Flessa, 1978); Equatorial Atlantic (Schott, 1935; Boltovskoy, 1964; Jones, 1967); South Atlantic (Boltovskoy, 1962; Loring, 1966); Antarctic (Blair, 1965; Herb, 1968; Kennett, 1969; Echols and Kennett, 1973); North and Equatorial Pacific (Bradshaw, 1959); Equatorial and South Pacific (Parker, 1960; Parker and Berger, 1971); Indian Ocean (Belyaeva, 1964; Bé and Tolderlund, 1971; Zobel, 1971; Bé and Hutson, 1977); Arctic (Vilks, 1973). For full references and review see Bé (1977). Although these studies substantially corroborate that water temperature is the principal cause for lateral variations in distribution, it has become 'more and more apparent' (Boltovskoy and Wright, 1976) that other factors are involved. As pointed out by Bé (1977), the standing stock of planktonic Foraminifera, as observed, is not only the result of a combination of environmental and biological factors but also a result of the artefacts that result from the level of sophistication of the sampling methods and laboratory procedures, including net and sieve sizes. The environmental factors include light, water chemistry, currents and turbidity and nutrients (phosphates and nitrates) as well as temperature. The biological factors include productivity (life span, growth rate and turnover), symbiotic relationships, competition and predation. Data on most of these factors are still lacking or sketchy.

The highest absolute numbers, per cubic metre of sea water, occur towards the equator and towards the poles and are associated with the main current gyres and regions of upwelling deep water. Numbers are at a minimum in central regions in mid-latitudes. Diversity and equitability are also high at the equator but low towards the poles and in central regions. This concentration is similar to that of other zooplankton and depends on the distribution of phytoplankton which in turn relates to nutrients. Populations are decidedly patchy. The highest total recorded is 100 000 per cubic metre at the 'oceanic front' off Baja California (Berger, 1969b). The daily 'flux' of dead tests apparently amounts to some 10 per cent of the living population. Most die after reproduction but also by displacement through mixing of different water masses. Predation also occurs by a range of macro-organisms, including euphausids, prawns, pteropods, crabs and salps.

The vertical range of individual species is wide and varies seasonally and regionally. A number probably adjust their depth habit during their life cycle. This means that the range is impossible to define within narrow limits. It is therefore 'statistical' and not a rigid stratification (Bé, 1977). Within the uppermost 200 m (epipelagic zone) the surface waters to 50 m are inhabited mainly by spinose species of *Globigerina* and *Globigerinoides;* the intermediate depths to 100 m by a mixture of spinose species of *Globigerinella* and *Orbulina* with smooth species of *Pulleniatina, Candeina* and *Neogloboquadrina;* depths below 100 m mainly by smooth globorotaliids which may spend their youth in the photic zone and then sink to lower depths. Live specimens have been taken down to 2000 m but have white protoplasm lacking symbionts and dead tests outnumber them

	Latitude	Temp. C.	MAJOR PLANKTONIC FORAMINIFERAL PROVINCES	
			DOMINANT SPECIES	SUBSIDIARY SPECIES
POLAR	+ 60°	< 5°	Turborotalia pachyderma (sinistral)	Globigerina bulloides† Globigerina quinqueloba Globigerinita bradyi† Globigerinita glutinata†
SUBPOLAR	50 - 60°	10 - 5°	Globigerina bulloides Globigerina quinqueloba Globigerinita bradyi Turborotalia pachyderma (dextral)	Globigerinita glutinata Globorotalia scitula Globorotalia truncatulinoides Turborotalia inflata†
TRANS.	40-50°	18-11°	Turborotalia inflata	mixture polar/subtrop. sp.
SUBTROPICAL	20 - 40°	24 - 19°	Globigerina falconensis Globigerina humulis Globigerinella aequilateralis Globigerinita glutinata Globigerinoides conglobatus Globigerinoides ruber Globorotalia crassaformis Globorotalia crotonensis* Globorotalia cultrata Globorotalia hirsuta Globorotalia truncatulinoides Hastigerina pelagica Orbulina universa	Globigerina bulloides Globigerina rubescens Globigerinoides sacculifer Neogloboquadrina dutertrei Pulleniatina obliquiloculata Turborotalia inflata
TROPICAL	0 - 20°	30 - 25°	Beella digitata Candeina nitida Globigerina rubescens Globigerinella adamsi* Globigerinoides sacculifer Globorotalia cultrata Globorotalia theyeri Globorotalia tumida Hastigerinopsis digitiformans Neogloboquadrina dutertrei 'Neogloboquadrina' conglomerata* 'Neogloboquadrina' hexagona* Pulleniatina obliquiloculata	Globigerina cf. bulloides Globigerinella aequilateralis Globigerinita glutinata Globigerinoides conglobatus Globigerinoides ruber Globorotalia crassaformis Globorotalia truncatulinoides Hastigerina pelagica Orbulina universa

Figure 14.8 Modern planktonic foraminiferal provinces. Latitudinal and temperature limits approximate only. *Occurrence in Indo-Pacific Region only; †subpolar or polar only in southern hemisphere. Data from Boltovskoy and Wright (1976) and Bé (1977)

below 500 m. Most individuals occur in the photic zone, to 120 m, with the richest levels between 10 and 50 m, but this varies locally and with the seasons. Cold-water forms may occur at depth in low latitudes — the phenomenon of 'tropical submergence'.

Vertical migration in the plankton, especially the tendency for a diurnal movement with a rise at night, is well known. Sampling difficulties have meant that so far it remains controversial in the planktonic Foraminifera. However, work carried out by N. Holmes of U.C.W. Aberystwyth in the summer of 1980 confirms the original conclusion of Owen (1867) that planktonic forams also generally rise at night.

Seasonal variations in numbers are the rule and linked to cycles in water chemistry and hydrology and related phytoplankton blooms. These blooms occur in winter in equatorial waters, in spring and autumn in temperature latitudes and in summer in the polar regions.

The strong latitudinal bias in the major planktonic communities is well shown in figure 14.8. Essentially there is a low latitude warm water community and a high latitude cold water community with a transitional zone of overlap in temperate regions. Each community can be split into two, giving tropical, subtropical, transitional, subpolar and polar communities which are duplicated in both hemispheres. The latitudinal limits are very approximate as there is a general tendency for the major current systems to carry cold faunas south on the east sides of continents and warm faunas north on the west sides of continents, in the Northern Hemisphere, with the reverse in the Southern Hemisphere. This means that the transitional fauna reaches 20°S off the west coast of South America and 65°N off Norway.

There are some 33 species of Recent planktonic Foraminifera, of which about 25 occur in the tropics and subtropics. The fall in diversity polewards is therefore dramatic, although highest diversities actually occur in the transitional zone which has mixed communities dependent upon currents and water mass contacts.

Although the duplication of the provinces in the two hemispheres strongly indicates interaction with surface temperatures, anomalies that show that the relationships are more complex include the greater tolerance of *Globigerina bulloides, Globigerinita bradyi, G. glutinata, Globorotalia scitula* and *G. truncatulinoides* to cold polar and subpolar waters in the Southern Hemisphere. In the restricted Arctic Ocean, virtually only *Turborotalia pachyderma* and *'Globigerina' quinqueloba* penetrate water below 5°C. There are also a number of 'relict' species such as *'Neogloboquadrina' hexagona,* and *'N' conglomerata* in the Indian Ocean which may reflect geological history, like the absence of *Pulleniatina obliquiloculata* from the Mediterranean. The bipolar distribution of species such as *T. pachyderma* undoubtedly also reflects historical causes (i.e. a more widespread distribution in the U. Miocene and later adaptation to cold polar waters).

Although most species appear to require oceanic salinities near 35 – 36 per thousand, *Globigerina bulloides, Globigerinoides ruber* and *Turborotalia pachyderma* can tolerate salinities down to 30.5 per thousand and can thus penetrate coastal waters if sufficiently clear and lacking in turbidity. Detailed mapping of individual species in the Indian Ocean shows the following apparent preferences:

T. pachyderma—low temperature and salinity, high oxygen and phosphates.

G. bulloides—warmer with higher salinity, low oxygen and phosphates.

'N.' hexagona—high temperature, relatively low salinity and oxygen.

G. truncatulinoides, G. rubescens, O. universa—intermediate temperatures, high salinities but low phosphates.

It is perhaps not surprising that in the light of these multifactorial responses the table (figure 14.8) shows considerable overlap of ranges. For instance, although *G. sacculifer* is generally the single most abundant species in the tropics, locally it is replaced by *G. ruber,* the dominant subtropical form. Clearly, temperature, although important, cannot be considered the 'overwhelming' factor.

APPLICATION IN PALAEO-ECOLOGY

The discovery of the strongly marked latitudinal distribution of the major planktonic foraminiferal communities by the 'Challenger' Expedition and the work by Pearcey (1890), which showed that the differences between the planktonics in the sediment on either side of the Wyville-Thomson Ridge could be related to temperature differences in the water masses, led eventually to application in palaeo-ecology. This began with Philippi (1910) who was able to show that there was an inverse relation between *G. cultrata* (*menardii* of authors) and *G. bulloides/T. inflata* in cores taken by the

German South Polar Expedition, 1901 – 03. Later, Schott (1935) was able to show that 1 m cores taken by the German 'Meteor' Expedition in the Equatorial Atlantic could be correlated on the basis of the whole fauna and that the absence of *G. cultrata* towards the middle of the cores could be explained as representing the last glacial period. The presence of *G. cultrata* in the lower part of the cores and at the top could be equated with the last interglacial and the Holocene.

These results quickened interest in the possible applications of planktonic Foraminifera in Pleistocene stratigraphy and climatology, but the limitations of gravity coring meant that only the top part of the succession was accessible. The invention of the piston core sampler (Kullenberg, 1947) overcame these difficulties and it was used successfully on the Swedish 'Albatross' Expedition to take cores up to 15 m length. Most, if not all, of the deep-sea Quaternary succession now came within reach of the stratigrapher. Attempts to read the history of the waxing and waning of the ice-caps in the foraminiferal succession (vertical changes being interpreted as caused by lateral shifts of the populations) now multiplied apace and burgeoned further when cores from the 'Glomar Challenger' became available from 1968. See Boltovskoy and Wright (1976) and Ruddiman (1977).

The methods of faunal analysis employed include:

(1) Study of the full assemblage and assessment of the relative abundance of species from the warm and cold communities.

(2) Use of species or species group abundance ratios. This is a development of Philippi's approach. Ericson, Ewing and Wollin (1964) similarly used the relative abundance of *G. cultrata* versus *T. inflata*. Lidz (1966) used *G. cultrata* versus *Sphaeroidinella dehiscens* and *T. inflata* versus *G. ruber*, while a variety of other combinations were used by Herman (1965, 1970).

(3) Relative abundance of a single species. This is a development of Schott's use of *G. cultrata*. The *G. cultrata* group was used by Ericson *et al.*, while *G. cultrata* s.s. was preferred by Lidz. Herman (1970) used *G. sacculifer* as an indicator of warm water and *T. pachyderma* has been used as a cold-water indicator by Devereaux, Hendey and Vella (1970).

(4) Use of infraspecific morphological features which include increased size and chamber number under optimum conditions in preferred water masses. This has been noted in *T. pachyderma* by Kennett (1968) and Vilks (1975) and in *G. bulloides* by Bandy (1972). It is also well displayed by tropical species such as *Orbulina universa* (Hecht, 1974; Hecht *et al.,* 1976).

There are many difficulties facing unambiguous interpretation of the results derived from such studies as evidence of climatic change. First, there are those which may be considered largely biological. As noted above, the communities are related to a complex of environmental factors, and relationship to temperature is clearly not fixed in many species (Cifelli, 1971). Species may have changed their optimum requirements with time and some modern associations may not be climax communities. Depth stratification and mixing may be impossible to distinguish from differences caused by climatic change and shifts in water masses and current systems may be considered, incorrectly, as of global significance.

In these circumstances it is best if interpretations are based on the maximum information available. This was the conclusion drawn by Boltovskoy (1973b) after a comparison of the results derived by use of different methods on cores from the South Atlantic. Although much more time consuming, the study of the whole fauna best revealed the degree of climatic change together with the finer oscillations. Use of species ratios, such as *G. cultrata* versus *T. inflata* apparently exaggerated the degree of temperature oscillation.

Secondly, there are difficulties caused by solution and diagenetic changes affecting the death assemblage when deposited on the deep-sea floor. As explained earlier, the settling rate of dead tests is quite rapid and it is assumed that little solution takes place on the way to the bottom although very small and light spiny forms may be selectively removed by currents. However, at depth all calcareous sediments are subject to some solution (Ruddiman, 1977). It has also been previously stated that the CCD, where all calcite goes into solution, is found at an average depth of some 4500 m but it is actually very variable depending on local conditions (see map in Berger and Winterer, 1974). Factors influencing it are productivity and sedimentation rate, the degree of undersaturation, oxidation and current speeds. Thus although the CCD may be as deep as 5000 m in the Equatorial Atlantic and South Pacific, it is generally shallower towards the shelves and particularly towards Antarctica where it may occur at less than 2000 m. This means that the lysocline, the zone at which appreciable changes in the proportion of species takes place (Berger, 1968, 1971a, 1971b) some hundreds of metres above the CCD, is equally variable. Experiments carried out by Adelseck (1977) show that a weight loss of up to 80 per cent occurs before the lysocline is reached, so significant solution occurs before there are detectable changes in the fauna (the point where 50 per cent weight loss occurs is called the R_0 level). Parker and Berger (1971) have ranked species according to their resistance to solution. The lighter, more porous and spinose species of *Globigerinoides* and *Globigerina* are most susceptible but individual species show considerable variation and smaller specimens of *G. ruber* are more resistant than the highly susceptible adults. Adelseck has derived an equation from morphological features to rank different species and calculated an assemblage solution index (ASI) to characterise entire assemblages.

Changes that can be attributed to solution were found in six cores taken in the Equatorial Atlantic (Ruddiman, 1971). In particular, *G. tumida* increased and *G. ruber* decreased with increasing depth. This change was most marked in the warm intervals (interglacials). However, as Ruddiman points out, this probably indicates that susceptible forms were relatively more abundant then, rather than that the CCD was actually raised in interglacial periods.

Fortunately, although the lysocline tends to be shallower in high latitudes its affects can be largely disregarded because the cold water fauna is more uniformly resistant (Ruddiman, 1977). The problem is most severe in equatorial regions where susceptible species are dominant in the water column but depleted in the sediments.

Difficulties are also caused by very slow sedimentation rates in some areas, with consequent condensation and increased vertical mixing of the assemblages by burrowing infauna. The resolution possible, taking into account the sedimentation rates in different oceans, has been calculated by examination of the mixing of tektites and ash bands (Ruddiman, 1977). In the North Atlantic, ash shards are dispersed through some 50 cm of sediment with decreasing abundance up and down from a point of peak abundance which represents the original pure ash band. Ninety per cent of the ash shards in each band is usually concentrated in less than 40 cm of sediments. As the average sedimentation rate in the North Atlantic is 4 cm/1000 y, this represents less than 10 000 y accumulation. Ruddiman supposes that if short volcanic events represented by only 0.1 cm average thickness of original sediment are still detectable, then peak abundances in the planktonic record lasting more than 1000 – 2000 years should be readily recognisable. Obviously, this will be much more difficult where sedimentation is very slow, as in most of the Indian Ocean, and Pacific Ocean, less than 1 cm/1000 y, and matters will be made worse by intervals of non-deposition and erosion. Areas with sedimentation rates above 3 cm/1000 y are therefore considered optimal for detailed palaeoclimatic resolution. The shape of graphed curves for glacial and interglacial periods should be distinguishable with intervals as short as 4000 y accurately recorded. Sedimentation rates of 1 cm/1000 y are regarded as at the limit of resolution for 10 000 y episodes. This means that most of the Indo-Pacific Ocean succession is unsuitable for detailed palaeoclimatic work, whereas most of the Atlantic succession is suitable, especially the North Atlantic, as is the Mediterranean.

Thirdly, there is the difficulty of dating climatic events in the Quaternary which lacks a detailed, relative time-scale based on evolutionary events because time is too short. Palaeomagnetism provides only a guide control because the two main scales (Rona and Emiliani, 1969) and Broeker and Ku (1969) differ by 25 per cent (Ruddiman, 1977). This has led to use of isotopic temperature curves (see below) being used as stratigraphic markers but there is, of course, grave objection to the use of a relative temperature scale being used as a time-scale, involving, as it does, the strong possibility of circular reasoning.

SPECIAL METHODS

The difficulties experienced with relative abundances of species in palaeoclimatological research have led workers to place weight on morphological features which cut across other taxonomic features and seem to be strongly related to climate. For instance, both cold- and warm-water species appear to exhibit increased shell porosity in warmer water (Wiles, 1967; Bé, 1968; Frerichs *et al.*, 1972). In *Turborotalia pachyderma,* increased porosity also seems to be related to the presence of reticulate rather than rugose ornament, although not in the Miocene, which may indicate an evolutionary difference in the later forms (Dow, 1977). The difference in ornament between specimens of *T. pachyderma* from colder and warm water was also noticed by Srinivasan and Kennett (1974).

A phenomenon that has excited general interest is the tendency for planktonic forams to show a preferred direction of coiling with switches in coiling direction (Bolli, 1950, 1957b, 1971; Bandy, 1967) that can be related to climatic or other environmental effects. The remarkable dominance of sinistral *T. pachyderma* in polar waters and dextral specimens in subpolar waters (figure 14.8) is a well-known example (Ericson, 1959) and has been applied as an indicator of climatic change in the Plio-Pleistocene of both California (Bandy, 1960b) and New Zealand (Jenkins, 1967). A coiling switch in this species from dextral to almost 100 per cent sinistral, lasting up to 9500 years, detected in North Atlantic cores has also been used as evidence of an intense cold phase at about 195 000 B.P. (McIntyre *et al.,* 1972). However, it must be pointed out that some workers, such as Olsson (1974), have found that the proportions of dextral to sinistral individuals were not very successful in identifying cold cycles and Vella (1974) claimed that the proportions differed in different size fractions. Again, although *Globigerina bulloides* shows a similar pattern of coiling distributions in the modern ocean the trend is more gradational (Boltovskoy, 1973b) and *Globorotalia truncatulinoides* shows a confused picture in both hemispheres that cannot be related to temperature (Boltovskoy and Wright, 1976). On the other hand, some coiling changes are clearly widespread, for instance the *Globorotalia (T.) praescitula* lineage switches from random to left coiling at the same time in the Lower Miocene in New Zealand and Australia (Walters, 1965; Jenkins, 1971a). Similarly, Saito (1976) has shown that switches of coiling direction in *Pulleniatina obliquiloculata* were concordant throughout the world oceans in the early Pliocene but became discordant in the Atlantic after the closing of the Panama marine connection in the late Pliocene. It is interesting, that in his investigation of coiling directions throughout the history of the Globigerinida, Bolli (1971) reveals that early stocks showed no preferred coiling directions and that the main switches, to either right or left coiling, occurred during the main warming trends discussed earlier, when diversification reached its height. Among the different families, only the Globotruncanidae appear to have become wholly dextral. The reasons for this phenomenon are obscure, although presumably coiling in one direction facilitates plastogamy and drifting together rather than apart.

The presence of a keel, although different from the special features discussed here, in that it is normally considered of generic significance, is also taken as an indication of a warm climate and Bandy (1964) defined a 'keel line' at 17°C (more or less the boundary between subtropical and transitional waters) with only turborotaliids present in temperatures below this to 9°C. Although there are exceptions to this 'rule', in that *G. truncatulinoides* penetrates Antarctic waters, there is no doubt that the keeled globorotaliids, *Globorotalia* s.s., are typical representatives of the warm assemblage today and apparently in the past. Jenkins (1973a) pointed out that keels appear to develop at different rates in different water masses and are apparently related to warming trends.

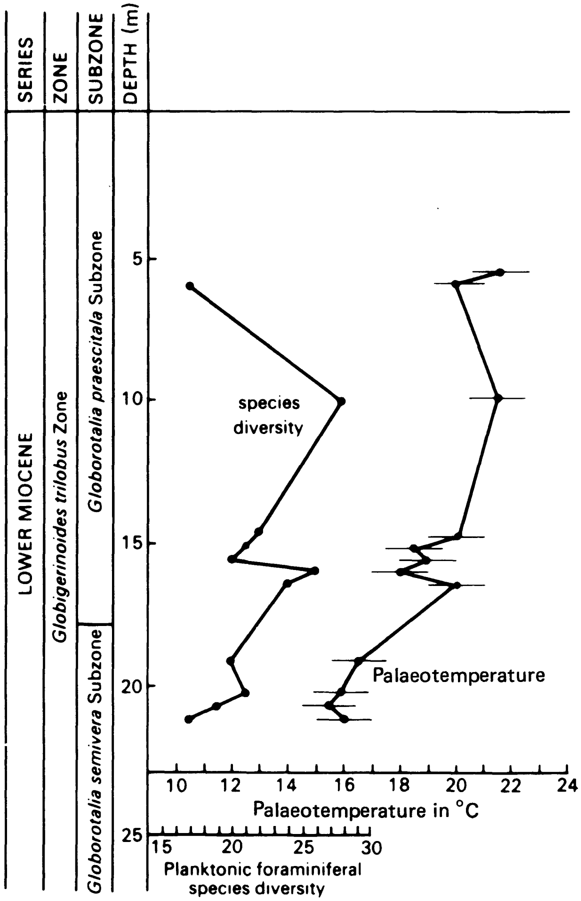


Figure 14.9 Isotopic temperature and diversity of Lower Miocene planktonic Foraminifera in Sea Lab Trial borehole, English Channel. From Jenkins and Shackleton (1979)

As discussed earlier, there is a marked general fall in planktonic foraminiferal diversity towards high latitudes and if it is kept in mind that factors other than temperature are involved, as shown by the fall of diversity in nutrient poor central regions, and that reversals may occur, as in the transitional province due to mixing of communities, then it can be used as a general climatic indicator (Jenkins, 1973b; Olsson, 1974; Poore and Berggren, 1974). Cifelli and Smith (1974) have argued against its use but it appears to be valuable when combined with other evidence. In this connection, the work of Jenkins and Shackleton (1979) which relates diversity to oxygen isotope temperature in borehole samples from the English Channel is very interesting (figure 14.9). Although the curves show a general match, the detailed relationship is 'remarkable' in that taken from the base upwards; although five of the samples show a rise of diversity (species number) with a rise of isotopic temperature, in the other five a rise is matched with a fall, or a fall with a rise. Again, although the sample with the highest estimated temperature shows the most species (28), one of the samples with the next highest temperature shows the (equal) lowest number. These results could be interpreted as representing a passage from the Transitional Province (low temperatures and low numbers) to the boundary of the Subtropical Province (high temperatures +18°C, and fluctuating numbers due to mixing of water masses), despite the lack of keeled globorotaliids. See below for discussion of isotope analysis.

Quantitative Methods with Use of Transfer Functions

A number of workers have introduced statistical methods involving the use of algebraic equations (transfer functions) in an attempt to increase the accuracy and objectivity of comparisons between modern assemblages, in which the temperature and other environmental limits are known, and their fossil counterparts. As in the simple methods described above, application has been to whole faunas (species regression) with environmental data based on a factor analysis of living assemblages (Lynts and Judd, 1971) or on the death assemblage in the sediment (Imbrie and Kipp, 1971); and to the principal components (principal component regression) of the assemblages (Imbrie and Kipp, 1971). It has also been applied to comparison of core top samples taken at increasing distances from a reference sample (distance – index regression), by Hecht (1973a), to diversity changes in core top samples (diversity – index regression), by Williams and Johnson (1975), and to samples in which the characteristic temperature of each species is determined (weighted average regression), by Jones (1964).

To avoid large errors, Kipp (1976) has warned against the use of these equations on samples in which species abundances exceed those in the original samples on which the equations were based. Likewise, algebraic experiments carried out by Hutson (1977) show that results are likely to be in error when these equations are applied to assemblages without modern analogues. Only the weighted average technique does not extrapolate and therefore may provide the best 'guess' of temperature. However, this technique, when applied to South Atlantic assemblages using an equation based on North Atlantic data, consistently underestimated summer temperatures and overestimated winter temperatures and required a correction factor (Berger and Gardner, 1975; Berger and Roth, 1975).

Relative Abundance of Planktonic and Benthonic Foraminifera as an Indication of Depth

Because planktonic Foraminifera are typical of the pelagic realm and the proportion of their dead tests in the sediment generally decreases markedly over the shelves and close to shore, various workers have attempted to use the relative abundance of planktonic and benthonic Foraminifera as an indication of depth and of the proximity of open, oceanic conditions (Israelsky, 1949; Smith, 1955; Grimsdale and Morkhoven, 1955; Stehli and Creath, 1964; Tipsword, Setzer and Smith, 1966; Kafescioglu, 1975; Murray, 1976; Marks, 1979).

Planktonic foram percentages above 70 per cent are found on the lower Continental Slope and on the Abyssal Plain, with well-developed life assemblages and large adults, and fall to less than 50 per cent on the Outer Shelf, with increasing dominance of far-drifted juveniles and falling diversity. However, the percentages are locally very variable. Thus, Grimsdale and Morkhoven found that an accurate trend with depth could not be established in the Caribbean, and Marks, who studied samples along a transect down the Hebrides Terrace into Rockall Trough, N.E. Atlantic, found that there was only a 'vague' relation of both percentages and maximum sizes to depth.

The percentages found in a particular sample depend on a number of factors:

(1) Productivity and sedimentation rates. The productivity of the planktonic and benthonic faunas are usually independent variables but may be positively correlated in some instances, as when

the Globigerina Ooze affords a preferred substrate for certain species.

(2) Proximity of oceanic waters to coastal regions and an onshore direction of residual currents, allowing penetration of low salinity species and a larger influx of dead, drifted tests. The higher percentages of planktonics on the Outer Shelf in the Celtic Sea (Murray, 1976) compared to those on the Outer Shelf in the Gulf of Mexico (Tipsword *et al.,* 1966) appears to reflect the strength of the Gulf Stream.

(3) Mixing of water masses. The erratic percentages and size variations recorded by Marks in Rockall Trough can be largely explained as due to the effects of the interplay of four or five major water masses—Upper Saline Layer, Intermediate Gulf of Gibraltar water, Labrador water and a deep, mixed layer of both Norwegian and Atlantic Deep water.

(4) The amount of solution that may have taken place above the lysocline (see above) and the possible different responses of the planktonics and calcareous benthonics.

(5) The different response of planktonics and benthonics to current transport and abrasion.

(6) The sieve-size limits chosen. A 63 μm (240 mesh) sieve is required to catch juveniles or the numbers will be underestimated on the Shelf.

It is therefore, clear that the relative abundance of planktonics cannot be used as a simple, direct guide to depth, but when used in concert with other information and, preferably, with study of the whole foram fauna, can be an aid in palaeogeographical reconstruction.

STABLE ISOTOPE ANALYSIS OF PLANKTONIC FORAMINIFERA

Molluscs grown in tanks where the temperature and oxygen isotope composition (relative proportion of the stable isotopes, ^{16}O and ^{18}O) is controlled have been shown (with one exception) to secrete calcium carbonate in isotopic equilibrium with the water. The relative abundance of the isotopes in the shell, analysed by mass spectrometer, is therefore, apparently, a function of both the temperature and the isotopic constitution of the water. This relationship has allowed the formulation of an empirical, carbonate/temperature equation that can be used as a geothermometer to estimate palaeotemperatures (Urey, 1947, 1948; Epstein *et al.,* 1951, 1953; Craig, 1965; Shackleton, 1967, 1974).

In the case of Recent shells, where the isotopic composition of the sea can be measured, the temperature can be estimated directly. In the case of fossil shells, where the oxygen isotope composition of the sea is unknown, the equation gives the deviation (and the value) from a known standard, based on the rostrum of a Cretaceous belemnite, B-1, from the Pee Dee Formation of South Carolina. The ^{18}O content of the standard, PDB-1 (Chicago) is +0.20 per thousand, relative to standard mean ocean water (SMOW). This means that analysis can show whether the sample represents water colder or warmer than the standard, provided that the difference is not mainly due to changes in isotopic composition. Additional standards have been set up by Shackleton (1974).

Although other invertebrate groups such as echinoderms and corals show 'vital effects' and do not appear to fractionate oxygen isotopes in equilibrium with the ambient sea water, this equation has been applied to Recent planktonic Foraminifera with results that are claimed to be in accord with the temperatures in which they actually grew. This has allowed Emiliani to investigate the depth stratification of planktonic species and to measure the temperature changes recorded by species in deep-sea cores (Emiliani and Epstein, 1953; Emiliani, 1954, 1955, 1956, 1958, 1964, 1966a, 1966b, 1970, 1971a, 1972, 1974). In particular, he was able to show (1955) that the temperature of the surficial tropical waters has apparently periodically oscillated some 5 – 6°C, with 7 cycles discernible in the Caribbean and 15 in the Pacific since the beginning of the Pleistocene.

The success of this work in indicating the worldwide fall in temperatures during the Tertiary and the fluctuations of the Pleistocene has stimulated a large number of other investigations, especially after the advent of the JOIDES programme; some of these investigations also include analysis of the benthonic Foraminifera (Lidz *et al.,* 1968; Shackleton, 1968, 1974, 1977a, 1977b; Devereaux, Hendy and Vella, 1970; Douglas and Savin, 1971, 1973, 1978; Herman, 1972; Hecht and Savin, 1972; Donk, 1973; Saito and Donk, 1974; Shackleton and Kennett, 1975a, 1975b; Cline and Hays, 1976; Kellogg *et al.,* 1978, among others).

Especially significant are the temperature curves for the last 125 000 years constructed by Hecht (1973b). These support the work of Emiliani in indicating 5 – 6°C variations in the surface waters of the equatorial Atlantic and Caribbean and also suggest 3 – 4°C variations in the Gulf of Mexico.

In addition, the work of Vernaud Grazzini (1975) on four long cores from the Mediterranean, suggests that the glacial/interglacial variation in temperature over the last million years in that area was not more than 11°C. Twenty-two cycles have now been recognised in Pacific sediments representing the last 870 000 years (Shackleton and Opdyke, 1973) and 42 for the Quaternary as a whole (Hecht, 1976b).

Depth stratification of planktonic species has apparently existed since the Mesozoic, with most species living in the uppermost 150 m. Subspecies and infraspecific variants may inhabit different depths, and forms of *Globigerinoides ruber* with small last chamber (kummer forms) are presumed to live in colder, deeper water than the normal forms (Hecht and Savin, 1972). Double-keeled species of *Globotruncana* are 'isotopically lighter' than single-keeled forms and apparently lived at shallower depths. Heterohelicids were both shallow and deep dwelling (Douglas and Savin, 1973). The clear distinction between the isotopically light globotruncanids and their allies and the isotopically heavy benthonics gives the first independent evidence that they were, indeed, planktonic (Saito and Donk, 1974). Similarly, most species of *Globorotalia* occupied deeper habitats than species of *Globigerina* and *Globigerinoides* (Douglas and Savin, 1978).

The results of the study of both planktonic and benthonic Foraminifera from the Maastrichtian and Danian in the South Pacific by Saito and Donk, are also of great interest considering the long controversy about the 'massive extinctions' at the Cretaceous/Tertiary boundary. The temperature of the surface water in the late Cretaceous was similar to today but the bottom water appears to have been much warmer than today, by rather more than 10°C (14 – 15°C rather than 2 – 3°C)—a direct effect of mild, ice-free polar regions. A fall in temperature of about 3.5°C in surface waters and 5°C in bottom waters occurred during the late Maastrichtian and early Danian over a 4.5 m.y. interval. It then took another 4 m.y., until the beginning of the Thanetian, for temperatures to recover. Saito and Donk conclude that the timing of this climatic event with the extinctions in various taxa is 'sufficiently coincidental to suggest causal effect'. Oxygen isotope evidence from benthonic Foraminifera also suggests that the present deep, cold, bottom layer of oceanic water (psychrosphere) began to develop some 30 m.y. ago near the Eocene/Oligocene boundary (Kennett and Shackleton, 1976) with the initiation of the Antarctic Ice Sheet (22 – 38 m.y.). There was a further decline in the temperature of bottom waters to near present values in the late Middle Miocene (Savin *et al.*, 1975) when the Antarctic Ice Sheet was probably much more extensive than it is now (Shackleton and Kennett, 1975a).

Another application of the temperature values obtained from isotopic data is in the plotting of plate movements. Thus, Douglas and Savin (1973) have demonstrated a general northward movement over the equator of the DSDP sites 167 and 171 in the Pacific through the Tertiary, based on changing water temperatures.

These dramatic results are very good news for the palaeogeographer and stratigrapher. But despite the fact that they can be found to agree with temperature curves based on analysis of species present and other evidence (Barash *et al.*, 1973; Hecht, 1976), modern work also brings the bad news that interpretation of oxygen isotope ratios is much more difficult than was first thought.

Of prime importance is the question of possible 'vital effects' causing fractionation of oxygen isotopes out of equilibrium with the sea water. Work has proceeded on the assumption that these could be largely ignored, despite the highly perceptive suggestion of Frances Parker (1958) that oxygen exchange might occur in planktonic Foraminifera between calcium carbonate and oxygen liberated from symbiotic algae, giving non-equilibrium fractionation. It has now been shown (Shackleton, Wiseman and Buckley, 1973) that four species gathered from isothermal surface waters of the Indian Ocean do yield different oxygen isotope values. In one, *Globigerinoides ruber*, it is equal to an error of 2.5°C. Similar evidence of non-equilibrium fractionation in planktonic species has been found by Vernaud Grazzini (1976) and Khan (1977). It has thus become clear that 'a substantial portion of the variation in isotopic composition between one species and another in foraminiferal death assemblages is due to different fractionation factors rather than to different life habitats'. Further research on living planktonic Foraminifera is obviously required to see if these effects are specific and whether the values found for fossil specimens can be corrected. Correction will be difficult if a large error is introduced by the presence of symbionts, now known to be present in many planktonic species as well as in benthonics.

That other 'vital effects' besides the activity of symbionts also occur is shown by the recording of different isotope values in deep-sea benthonics from the same samples. Thus, although Smith and

Emiliani (1968) claimed that benthonic Foraminifera deposit calcium in equilibrium with sea water and this has been assumed for *Uvigerina* (Shackleton and Kennett, 1975b), other workers have found significant variations in specimens from the same core. Some species may give temperatures up to 5°C too high (Vinot-Bertouille and Duplessy, 1973).

Further difficulties are caused by the tendency of some planktonic species to move up and down in the water column during ontogeny, as mentioned earlier. Shackleton (1968) suggested that only surface-dwelling species should be used in analysis because the isotope values for migratory species may average the vertical temperature range. Unfortunately, it is the shallower species which are most likely to be symbiotic.

As suggested by Imbrie *et al.*, (1973), it is necessary to establish an empirical temperature scale for each species used in isotope analysis. A combination of the results with what can then be learned from the presence and percentage occurrence of extant species of known geographical range, will be the best practice. Examples of this more refined, combined approach include those of Cita *et al.* (1977) and Kellogg *et al.* (1978). It is noteworthy that in their work on a long core from the eastern Mediterranean, Cita and her co-authors find a close but not perfect fit between the faunal data and the ^{18}O curve.

A major problem in estimating palaeotemperatures by the isotopic method is that ^{16}O:^{18}O ratios have almost certainly changed with time. This is because the lighter ^{16}O is preferentially removed by evaporation; for instance, the W. Mediterranean has an isotopic composition 1.2 per cent higher than N. Atlantic deep water (Cita *et al.*, 1977). It is also preferentially built up in glacial ice. The isotopic composition of the sea therefore fluctuated during the Pleistocene with the waxing and waning of the great continental ice sheets. It is a matter of dispute what percentage should be subtracted from the values given by isotope analysis to allow for these changes. Emiliani supposed it to be some 30 per cent in arriving at his estimate of 5 – 6°C for the amplitude of the glacial/interglacial cycles in equatorial waters. But other workers, such as Olausson (1965), Shackleton (1968), Dansgaard and Tauber (1969), Imbrie *et al.* (1973) and Shackleton and Opdyke (1973), claim that a much larger part of the isotopic variation is due to changes in water composition, even up to 100 per cent. This would give much smaller temperature variations and the record from deep-sea cores can then be read, largely, as a measure of the growth and retreat of the ice sheets. Attempts to resolve these difficulties were made by Emiliani and Shackleton (1974) and Savin and Stehli (1974).

It is usually assumed that changes in the isotopic composition of sea water were negligible before the major extension of the Antarctic Ice Cap in the late Middle Miocene. But valley glaciers appear to have existed in Antarctica during the Middle Eocene (Margolis and Kennett, 1970). In a sense, then, the Cenozoic is coincident with the 'Ice Age'. This increases the importance of the attempt by Sommer *et al.* (1977) to devise a method which avoids the problem of the unknown isotopic composition of sea water by use of an equation based on the difference in fractionation between pairs of aragonitic and calcitic benthic Foraminifera.

Because the relative proportions of the stable isotopes of carbon, ^{12}C and ^{13}C, in the planktonic foraminiferal test can also be used for estimating temperature (Sackett *et al.*, 1965; Emrich *et al.*, 1970) carbon isotope analysis has increasingly been used as an adjunct to the oxygen isotope method (Saito and Donk, 1974; Williams and Sommer, 1975; Vincent and Shackleton, 1975; Boersma and Shackleton, 1977; Curry and Matthews, 1977; Williams *et al.*, 1977; Shackleton and Vincent, 1978; Berger *et al.*, 1978).

As observed by Shackleton (1977c), the carbon isotope composition of available inorganic carbon varies from place to place in the ocean, mainly as a result of production of organic carbon compounds which leaves the remaining inorganic carbon isotopically enriched. The depth profile varies according to dissolved oxygen and to the gradual oxidation of falling organic debris, with a sharp gradient in near-surface waters. An example of the way in which the ^{13}C 'stratigraphy' of the upper part of the water column may assist in the oxygen isotope analysis of the depth habits of particular species, is provided by the work of Williams and Sommer (1975) in the Indian Ocean. Oxygen isotope analysis indicates that *Globigerinoides ruber* occurs at a shallower depth than *G. sacculifer* in tropical waters but that this relationship is reversed at 30°S. The carbon isotope results are consistent with this interpretation which is encouraging, although because this research was based on core-top samples, further work on the living fauna is clearly necessary. Sackett (1978) has found systematic variations in ^{13}C in a long core in the South Pacific which can be correlated with migration of the South Polar Front. But he observes that disadvantages of the method included lack of knowledge of the factors which determine the carbon isotope composition in plankton, kerogen recycling near the Antarctic Continent and 'obliteration of the palaeotemperature signal' by deposition of land-derived plant material.

It will thus be seen that the application of oxygen isotopes, in studies of palaeotemperatures, even with the assistance of carbon isotopes, is not so precise as was at first hoped. As pointed out by Shackleton *et al.* (1973): 'It is not possible to translate the value obtained into an equivalent temperature on the basis of thermodynamic principles alone.' They also stress the more serious difficulty that different laboratories give different results for samples from the same material. For example, specimens of *Globigerinoides ruber* from the same core horizon gave temperatures ranging from 27°C to 32°C. This 5°C error is, of course, equal to the fluctuations being given for the Pleistocene. Although the analyses made by the laboratories may be internally consistent, errors of this magnitude preclude useful correlations between sections analysed by different laboratories.

It must be pointed out that, despite these difficulties, Shackleton (1977a) claims that the oxygen isotope curves for the late Pleistocene in most parts of the world ocean can be matched so precisely that the fluctuations can be used for long-distance correlation and as an 'ideal monitor of glacio-eustatic change'. However, as noted above, this depends on the assumption that the enrichment of ^{18}O in the oceans during the glacials (approximately 0.1 per thousand for every 10 m drop in sea level) is almost entirely due to the growth of the ice caps and that mixing takes place in less than 1000 years. Work on the late Pleistocene has the advantage that cross-correlation by means of carbon-14 dating, varve analysis and other techniques is possible, so further work will test the validity of these assumptions and whether the ^{18}O record is actually more time parallel than the fluctuations of species.

CONCLUSION

It is unnecessary to underline further the value and importance of planktonic Foraminifera in stratigraphy and palaeo-ecology. But the very success and burgeoning output of research on this outstanding group does highlight certain problems of scientific attitude, also considered in earlier chapters. Some of the pitfalls have been mentioned. I have tried to emphasise throughout that biological and palaeontological phenomena generally reflect multiple causes and the influence of many, often independent, variables. It is, therefore, unlikely that major problems of classification, biostratigraphy or palaeo-ecology will be turned by a single 'key', whether based on biological, physicochemical or mathematical criteria. A holistic approach is required and the micropalaeontologist must bring to bear all the evidence that can be gathered from the geological materials at his disposal together with what is known and can be learned from neontology.

The student must also remember that our conclusions are always provisional and subject to change or refutation—necessarily so, if they are to remain scientific and not degenerate into mere dogma. As Richard Jefferies put it a hundred years ago:

> The thoughts of man are like the foraminifera, those minute shells which build up the solid chalk hills and lay the level plain of endless sand; so minute that, save with a powerful lens, you would never imagine the dust on your fingers to be more than dust. The thoughts of man are like these: each to him seems great in his day, but the ages roll, and they shrink till they become triturated dust, and you might, as it were, put a thousand on your thumb-nail. They are not shapeless dust for all that; they are organic, and they build and weld and grow together, till in the passage of time they will make a new earth and a new life.

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SUMMARY CLASSIFICATION

MAIN FAMILIES AND IMPORTANT GENERA OF GLOBIGERINIDA

GLOBIGERINIDA	hyaline radial, characteristically coarsely bilamellar and perforate, surface textures spiny to smooth, reticulate or rugose; trochospiral to planispiral, biserial and spreading; chambers often globose and/or radially elongate; apertures enlarged or multiple with various accessory structures and coverplates; keels commonly developed; ? M. Jur. – Rec. Key figure 14.10, plates 2A, 14 and 15.
HEDBERGELLACEA (= Hedbergelloidea Longoria & Gamper 1975)	low trochospiral to conical, aperture ventral umbilical to extra-umbilical with narrow flaps (portici) which may be partially fused or fully joined to form a coverplate; Cret., Haut. – Maas. Key figure 14.10, plate 14.
HEDBERGELLIDAE (= Hedbergellinae Loeblich & Tappan, *nom. transl.* Longoria & Gamper 1975)	narrow umbilical flaps, without accessory apertures; Haut. – Maas.
Hedbergella (nos. 1/2)	rounded periphery; Haut. – Maas. (carinate or with imperforate peripheral band only = *Praeglobotruncana* (nos. 3 – 5), Alb. – Turon.; chambers radially elongate = *Clavihedbergella,* Apt. – Turon.; ornament of raised ridges in polygonal pattern = *Favusella* Michael 1972, Alb. – Cenom.).
ROTALIPORIDAE	umbilical flaps partially fused forming 'platform' or partial coverplate with marginal accessory apertures; Alb. – Turon.
Rotalipora (nos. 6/7)	periphery acute with single keel; U. Alb. – Turon. (rounded periphery = *Ticinella* (no. 8), Apt. – Cenom.; last whorl with rounded periphery = *Anaticinella* Eicher 1972, Cen. – Tur.).
GLOBOTRUNCANIDAE	umbilical flaps fused to form tegillum, characteristically with marginal and areal accessory apertures; Turon. – Maas.
Globotruncana (plate 14, nos. 11 – 14)	periphery truncate with double keel, Turon. – Maas. (periphery rounded with imperforate band and faint double keel only = *Archaeglobigerina* Pessagno 1967; periphery angular with single keel only = *Globotruncanita*).
Rugoglobigerina (plate 14, nos. 15/16)	periphery rounded, without keel or peripheral band; surface with meridional rugosities or costellae; Sant. – Maas. (with peripheral band and double keel = *Rugotruncana,* Camp. – Maas.; peripheral band and faint keel in last few chambers only = *Trinitella,* Maas.; clavate = *Plummerita,* Maas.).
Abathomphalus (plate 14, nos. 19/20)	periphery truncate with double keel; umbilicus closed and aperture extra-umbilical, coverplate a single structure (techo) with marginal accessory apertures only; Maas. (peripheral band only =

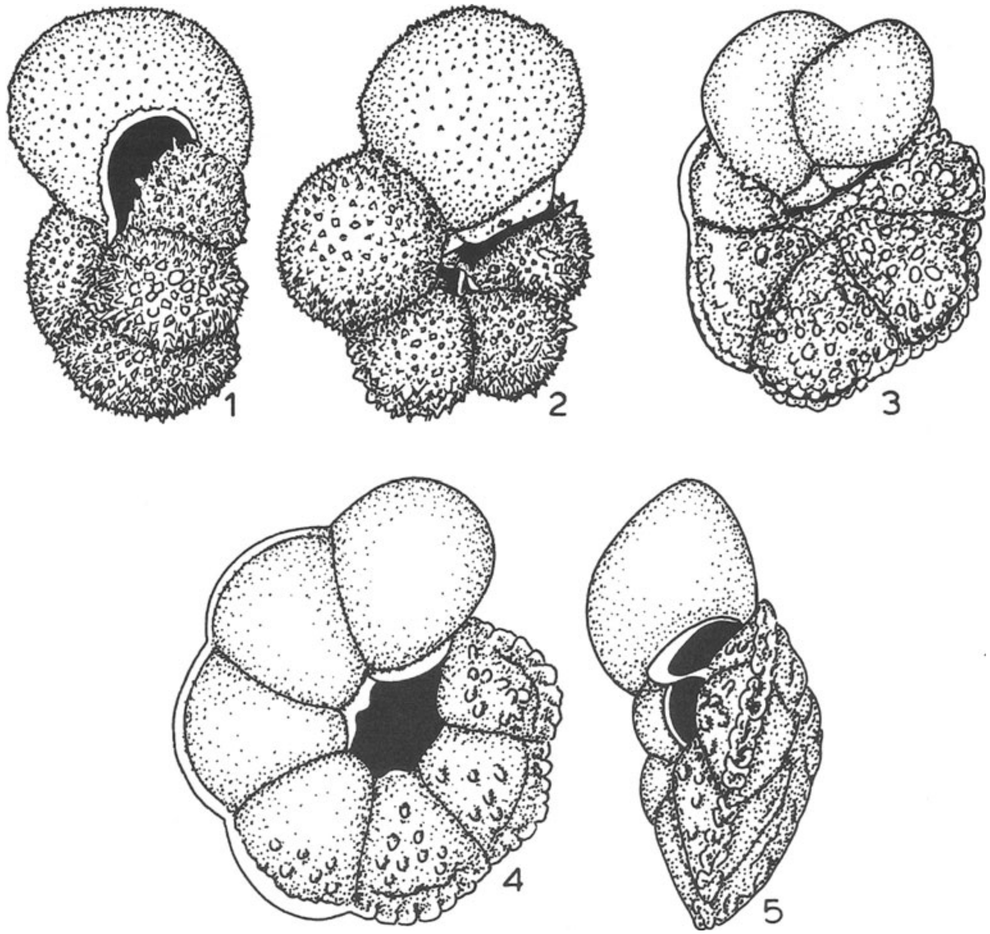
Globotruncanella, Camp. – Maas.). N.B. These genera have been placed in a separate family, Abathomphalidae, Pessagno 1967.

HETEROHELICACEA ALIJULLA 1977 (fide Grigelis 1978a)	trochospiral to planispiral, biserial and spreading; aperture median with narrow flaps (portici), lip or neck-like extension; L. Cret., Barr. – L. Mio. Key figure 14.10.
PLANOMALINIDAE	planispiral but may have trochospiral initial portion; primary median aperture with extensions into umbilicus which become 'relict' apertures as further chambers are added; ?Apt. – Maas.
Planomalina (nos. 9/10)	periphery acute with single keel; Alb. – Cenom. (periphery rounded = *Globigerinelloides* (no. 11), Apt. – Maas., with paired supplementary apertures also = *Biglobigerinella;* clavate = *Hastigerinoides,* Con. – Maas.).
SCHACKOINIDAE	trochospiral to planispiral; final whorls with hollow tubulospines or bulbous chamber extensions; U. Barrem. – Maas.
Schackoina (nos. 16/17)	chambers subspherical; single hollow tubulospines developed at periphery in the plane of coiling; aperture with lip; Apt. – Maas. (later chambers elongate with 1 or 2 bulbous extensions = *Leupoldina,* U. Barrem. – Cenom.).
HETEROHELICIDAE	planispiral to biserial, diverging and spreading with supplementary apertures and chambers; characteristically costate; Alb. – Maas. Key figure 14.10.
Heterohelix (nos. 12/13)	planispiral to biserial, at least in micro-gen.; chambers globular; aperture a high median arch with narrow lip; Alb. – Maas. (paired supplementary, sutural apertures along median line = *Pseudoguembelina* (no. 14), Sant. – Maas.; later chambers high with spinose projections = *Lunatriella* Eicher & Worstell (1970b), Turon.; adult thicker than wide = *Pseudotextularia,* Sant. – Maas.; adult uniserial = *Bifarina*).
Gublerina (no. 15)	compressed, wedge-shaped; biserial chambers diverging to give nonseptate central part which is finally divided by irregular secondary septa into small 'blister-like' secondary chambers; Camp. – Maas.
Ventilabrella (no. 21)	fan-shaped; early chambers biserial, later supplementary, sutural apertures develop at the periphery and supplementary chambers are added in the plane of biserial growth; Turon. – Maas. (round in section with supplementary chambers added opposite the biserial series and later chambers 'dumbbell' shaped = *Planoglobulina,* Maas.).
CHILOGUEMBELINIDAE Reiss 1963	biserial throughout; aperture with neck-like extension or collar; Palaeoc. – L. Mio.
Chiloguembelina (nos. 18/19)	chambers globular; Palaeoc. – L. Mio. (compressed with angular periphery = (*Chiloguembelinella* El-Naggar 1971).

GLOBIGERINACEA	trochospiral to streptospiral; aperture ventral umbilical to extra-umbilical, with characteristically symmetrical lip or umbilical teeth; advanced forms with discrete umbilical coverplates (bullae) and marginal accessory apertures; multiple apertures and supplementary sutural apertures often developed; ? Mid. Jur. – Rec. Key figure 14.10, plates 2A, 14 and 15.
GUEMBELITRIIDAE (= Guembelitriinae Montanaro Gallitelli 1957, *nom. transl.* El-Naggar 1971)	moderate to high trochospire, triserial to quadriserial chamber arrangement; rugose or with pore mounds; aperture umbilical with simple lip only; ? M. Jur. – Olig.
Guembelitria (no. 20)	high trochospiral, triserial, with pore mounds; L. Cret. – ? Maas. (rugose, without supplementary apertures = *Jenkinsina* n. gen., Palaeog., type species *Guembelitria stavensis* Bandy, here designated; quadriserial, moderate spire height, rugose = *Caucasella* Longoria & Gamper 1975, ? M. Jur. – L. Cret.; becoming spreading = *Guembelitriella,* Cenom.).
GLOBIGERINIDAE	low to moderately high trochospire (occasionally streptospiral) to embracing and unilocular; characteristically spinose and reticulate but may become smooth and pitted; chambers globose, may be radially elongate and digitate; aperture umbilical to slightly extra-umbilical usually with symmetrical lip which may be extended as an umbilical tooth; supplementary sutural apertures often developed on dorsal side; advanced forms may develop discrete coverplates (bullae) with marginal accessory apertures; Palaeoc. – Rec. Key figure 14.10, plates 2A, 14 and 15.
Globigerina (plate 2A, no. 3)	low trochospiral; chambers globular; surface spinose, pores countersunk leading to 'reticulate' ornament; aperture umbilical to slightly extra-umbilical, high arch with or without lip; Dan. – Rec. (chambers radially elongate = *Beella,* ? Quat.; bulla over umbilical area = *Catapsydrax* (no. 26), Eoc. – Mio.; last chamber acting as bulla = *Globigerinita,* Mio. – Rec.).
Globigerinoides (plate 15, nos. 1 – 5)	as *Globigerina* with supplementary apertures, often with moderately high spire; Dan. – Rec. (primary and secondary apertures with bullae = *Globigerinoita,* U. Mio.; irregular strip-like bullae and last chamber embracing with areal apertures and pustular bullae = *Globigerinatella,* L. Mio.).
Globigerinatheka (nos. 27/28, plate 14, nos. 3/4)	initially trochospiral but final chamber embracing and covering the umbilicus; numerous supplementary sutural apertures; bullae commonly developed covering apertures; M. – U. Eoc. (thick secondary wall, later chambers hemispherical = *Orbulinoides,* M. Eoc.). N.B. Nonbullate specimens formerly referred to *Globigerapsis.*

Sphaeroidinella (plate 14, nos. 7/8)	initial part like *Globigerina,* later chambers with thick, imperforate, secondary wall and flanges along sutures; one or more supplementary, sutural apertures; U. Mio. – Rec. (no supplementary apertures = *Sphaeroidinellopsis,* L. – U. Mio.).
Orbulina (plate 2A, no. 1)	initial part globigerine, at least in micro. gen., enclosed in a single, globular chamber with areal apertures; M. Mio. – Rec. (trochospiral with final chamber enclosing up to 75 per cent of test = *Praeorbulina,* L. – M. Mio.; bilocular or rarely trilocular = *Biorbulina*).
Candeina (plate 15, nos. 6/7)	moderately high trochospire of globular chambers; multiple, evenly spaced sutural apertures; late Mio. – Rec.
Pulleniatina (plate 14, no. 9)	initial part like *Globigerina,* later chambers streptospiral and overlapping with smooth wall, covering umbilicus; aperture displaced and extra-umbilical with thick lip; U. Mio. – Rec.
GLOBOROTALIIDAE	low trochospiral, biconvex or with dorsal side flattened; chambers subround or subangular to compressed carinate, may be radially elongate or produced ventrally; characteristically smooth to rugose but may be spinose; aperture largely extra-umbilical to entirely extra-umbilical, usually with a lip and may develop teeth; supplementary sutural apertures may be developed on dorsal side; Palaeoc. – Rec. Plates 2A, 14 and 15.
Globorotalia s.s. (plate 15, nos. 11 – 18)	biconvex or dorsal side flattened, periphery angular or carinate; surface smooth to rugose; L. Mio. – Rec. (small, relatively smooth forms from the Palaeogene have been referred to *Planorotalites;* angular conical forms with spiny keels to *Morozovella* McGowran 1968).
Turborotalia (plate 2A, nos. 2/4)	biconvex or with dorsal side relatively flat and ventral side strongly raised; periphery subround to subangular; surface smooth to rugose; M. Palaeoc. – Rec. (heavily spinose = *Acarinina,* M. Palaeoc. – M.Eoc.; supplementary sutural apertures also = *Truncorotaloides,* M. Eoc.).
Neogloboquadrina (plate 14, nos. 1/2)	biconvex with slightly flattened dorsal side; periphery rounded; chambers subglobular; surface smooth to rugose; aperture large, umbilical and extra-umbilical with both lip and umbilical tooth; late Mio. – Rec. (chambers produced ventrally and elongate in dorsal view, giving subquadrate outline = *Globoquadrina*).
HANTKENINACEA n. superfam.	asymmetric planispiral, with early trochospiral part, to streptospiral or planispiral; chambers globose to radially elongate or clavate and may be produced into tubulospines or bear terminal, triradiate spines; aperture ventroperipheral to median with lip, may extend to umbilicus on either side, these extensions remaining as 'relict' apertures as growth proceeds, may also extend into apertural face, 'triradiate', or becoming multiple and areal; U. Palaeoc. – Rec. Key figure 14.10; plates 14 and 15.

HANTKENINIDAE	asymmetric planispiral to planispiral; chambers globose, produced into peripheral tubulospines or clavate; advanced forms smooth with aperture extending as high slit into apertural face or areal; U. Palaeoc. – Olig. Key figure 14.10, plate 14.
Globanomalina (nos. 22 – 25)	asymmetric planispiral (with early trochospiral part) and tending to remain slightly evolute on former dorsal side with deep umbilicus on ventral; chambers slightly compressed to depressed; aperture a high arch, ventro-peripheral to median; Palaeoc. – Olig. N.B. Attempts have been made to distinguish fully planispiral forms as *'Pseudohastigerina'*.
Hantkenina (plate 14, nos. 5/6)	planispiral; biumbilicate; chambers with single, forward-directed peripheral spines; aperture median, 'triradiate', with basal arch and vertical slit, broad lips extending to umbilicus; M. – U. Eocene (without vertical apertural slit = *Aragonella*; secondary areal apertures above primary aperture = *Cribrohantkenina,* U. Eoc.; chambers bulbous without spines = *Clavigerinella,* M. – U. Eoc.).
HASTIGERINIDAE (= *Hastigerininae* Bolli, Loeblich and Tappan 1957, *nom. transl.* Saito *et al.* 1976)	asymmetric planispiral, with early trochospiral part, to streptospiral or planispiral; chambers globose, radially elongate or clavate; hispid to smooth with terminal, triradiate spines; aperture a wide, low arch, with thin lip; ? L. Mio. – Rec. Plate 15.
Globigerinella (plate 15, nos. 8/9)	asymmetric planispiral, with trochospiral initial part, to loosely coiled; hispid with mixed round and triradiate spines; adult chambers depressed; aperture ventro-peripheral to median in adult; L. Mio. – Rec. (chambers radially elongate = *Bolliella,* Rec.; surface smooth with triradiate spines at periphery = *Hastigerina,* Quat.; streptospiral and clavate with triradiate spines on chamber ends = *Hastigerinopsis* Saito *et al.* 1976, Quat.).

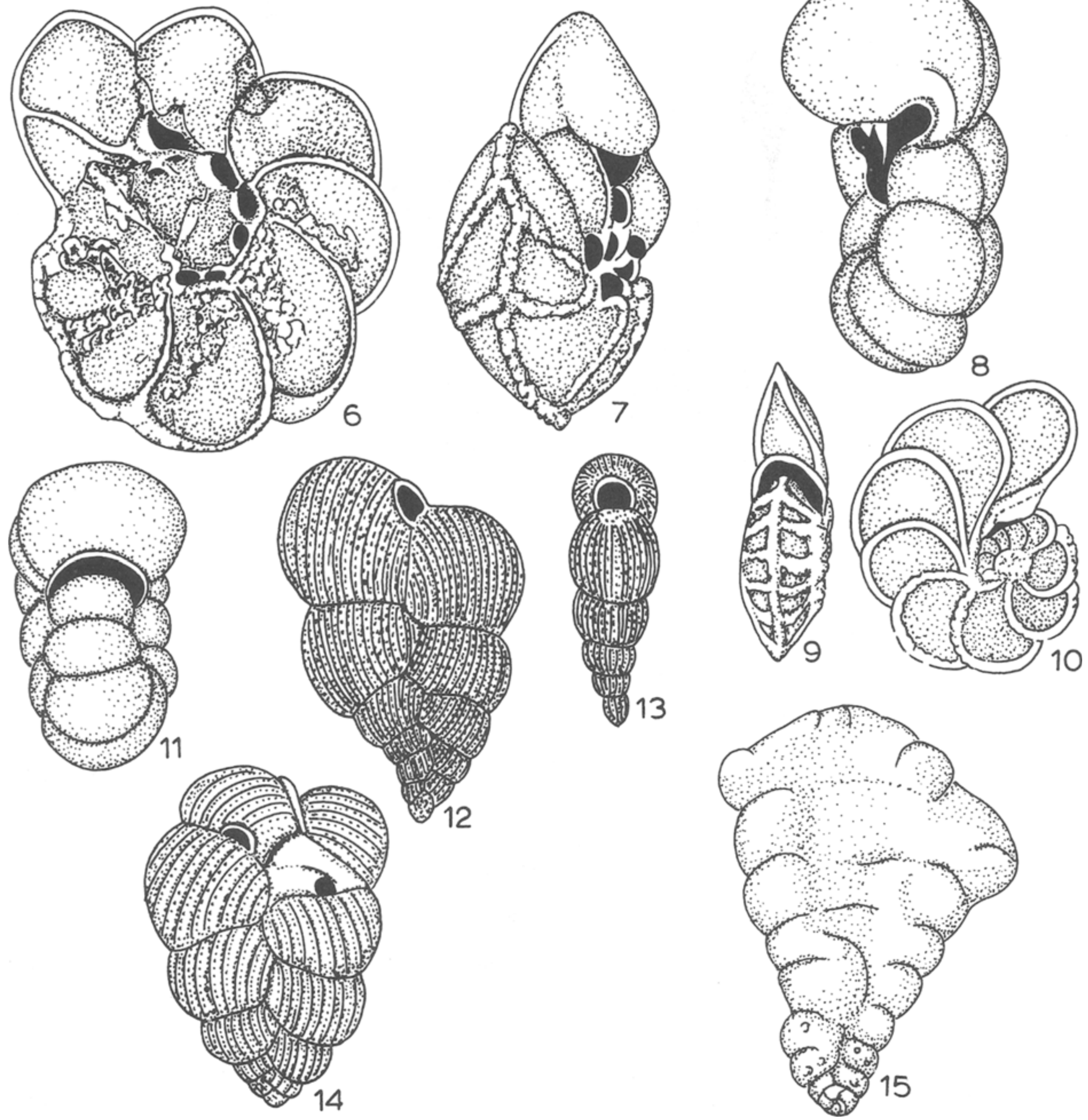


Key figure 14.10 **Globigerinida, Hedbergellacea, Heterohelicacea, Hantkeninacea, Globigerinacea**

1/2 ***Hedbergella delrioensis*** **(Carsey), peripheral and side views, after Michael, × 300**
3 ***Praeglobotruncana delrioensis*** **(Plummer), ventral view, after Michael, × 250**
4/5 ***Praeglobotruncana stephani*** **(Gandolfi), ventral and peripheral views, after Postuma, × 115**

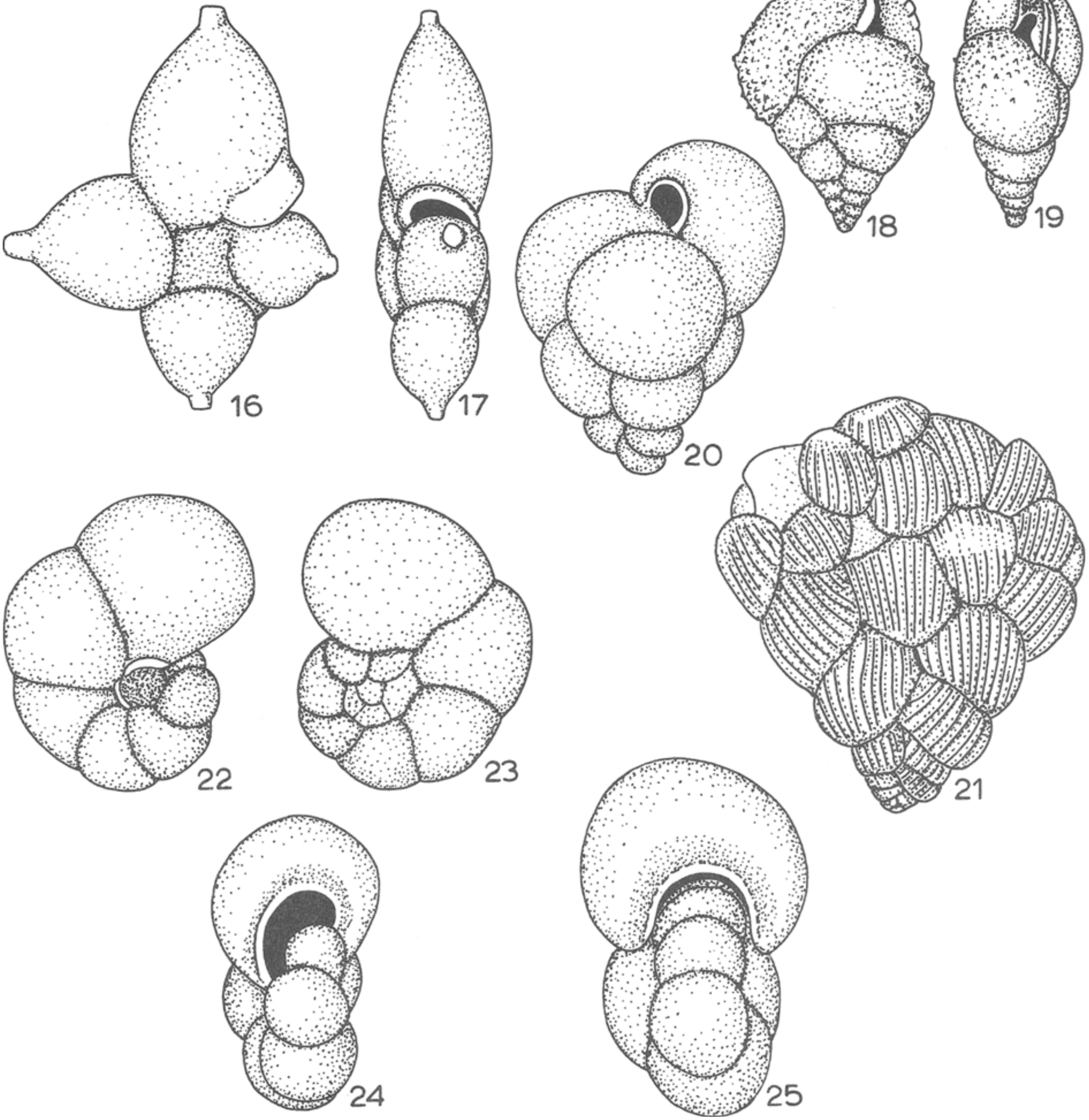
(continued overleaf)

Key figure 14.10 ***(continued)***



6/7 *Rotalipora greenhornensis* (Morrow), ventral and peripheral views, after Eicher, × 100
8 *Ticinella roberti* (Gandolfi), side view, after Postuma, × 115
9/10 *Planomalina buxtorfi* (Gandolfi), peripheral and side views, × 84
11 *Globigerinelloides breggiensis* (Gandolfi), peripheral view, after Postuma, × 100
12/13 *Heterohelix globulosa* (Ehrenberg), side and peripheral views, after Martin, × 120
14 *Pseudoguembelina excolata* (Cushman), side view, after Loeblich & Tappan, × 116
15 *Gublerina ornatissima* (Cushman & Church), side view, after Montanaro Gallitelli, × 74

Key figure 14.10 ***(continued)***



16/17 ***Schackoina cenomana*** **(Schacko), side and peripheral views, after Loeblich & Tappan, × 200**

18/19 ***Chiloguembelina midwayensis*** **(Cushman), side and peripheral views, after Loeblich & Tappan, × 100**

20 ***Guembelitria cretacea*** **Cushman, side view, after Loeblich & Tappan, × 312**

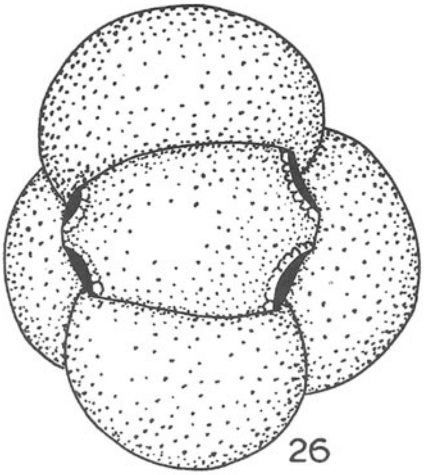
21 ***Ventilabrella eggeri*** **Cushman, side view, × 100**

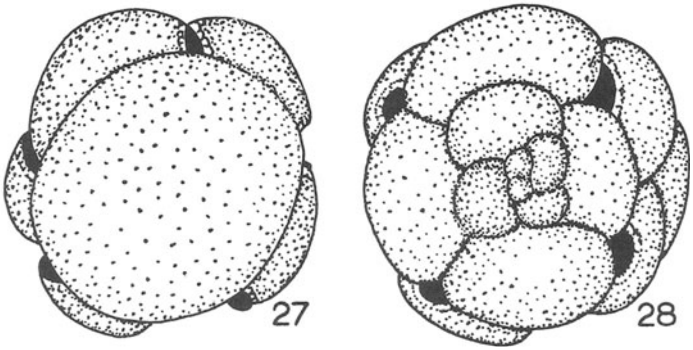
22–24 ***Globanomalina wilcoxensis*** **(Cushman & Ponton), ventral, dorsal and peripheral views of trochospiral form, after Berggren, Olsson & Reyment, × 150**

25 ***Globanomalina wilcoxensis*** **(Cushman & Ponton), peripheral view of planispiral form, after Berggren, Olsson & Reyment, × 150**

(continued overleaf)

Key figure 14.10 ***(continued)***





26 ***Catapsydrax dissimilis*** **(Cushman & Bermudez), ventral view showing bulla, after Postuma, × 130**

27/28 ***Globigerinatheka barri*** **Brönniman, ventral and dorsal views, after Postuma, × 130**

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Index

As I have attempted to demonstrate the interdependence of taxonomy and stratigraphy throughout the book, I have adopted the principle of 'the index, one and indivisible' (see G. Norman Knight, *Indexing, The Art of*, Allen and Unwin, 1979). Taxa are therefore not dealt with separately. Unimportant words at the beginning of subheadings are ignored in deciding the alphabetical arrangement. Authors' names are not indexed as they can be found by pursuit of the topics dealt with, which leads to the appropriate bibliographical references given in the text. Species may be found under generic heads and are not cross-referenced under their trivial names.

References to the text are in the following order: definitions of terms and diagnoses of taxa (page numbers in bold type) and the key illustrations are all in page order, with any other references then following. The term *passim* ('here and there') is used for discontinuous treatment.

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